# Current Bobcat Research and Implications for Management

*Symposium Proceedings*

from

The Wildlife Society 2000 Conference

Nashville, Tennessee
12–16 September 2000

**A. Woolf, C.K. Nielsen, and R.D. Bluett, editors**

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**Sponsors**:

Financial support for printing and preparation was provided by the Illinois State Furbearer Fund through a project submitted and further financed by the Cooperative Wildlife Research Laboratory, Southern Illinois University at Carbondale. We thank hunters and trappers who contributed to the Illinois State Furbearer Fund by puchasing Habitat Stamps.

**Illustrations**:

Photographs courtesy of Dr. Alan Woolf, Director of the Cooperative Wildlife Research Laboratory, Southern Illinois University at Carbondale.

**Suggested Citation Formats**:

Entire book
Woolf, A., C. K. Nielsen, and R. D. Bluett, editors. 2001. Proceedings of a symposium on current bobcat research and implications for management. The Wildlife Society 2000 Conference, Nashville, Tennessee, USA.

Paper in book
C. K. Nielsen, and A. Woolf. 2001. Bobcat habitat use relative to human dwellings in southern Illinois. Pages 40–44 *in* Woolf, A., C. K. Nielsen, and R. D. Bluett, editors. Proceedings of a symposium on current bobcat research and implications for management. The Wildlife Society 2000 Conference, Nashville, Tennessee, USA.

Abstract
Diefenbach, D. R., M. J. Lovallo, L. A. Hansen, R. J. Warren, and M. J. Conroy. 2001. Changes in spacing patterns with increasing population density of an insular reintroduced bobcat population. Page 80 *in* Woolf, A., C. K. Nielsen, and R. D. Bluett, editors. Proceedings of a symposium on current bobcat research and implications for management. The Wildlife Society 2000 Conference, Nashville, Tennessee, USA.

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# PREFACE

A colleague once referred to bobcats as "the louse of the Cat World." While unflattering, his characterization rings true in many respects. Like lice, bobcats are adaptable, resilient, and nearly ubiquitous.

Our work started with a different premise. Considered rare and confined to the southernmost part of Illinois, the bobcat was listed as a state threatened species when we launched a research project under the Federal Aid in Wildlife Restoration program. Believing the odds were in my favor, I made a friendly wager which pitted researchers against a goal of radio-collaring 20 individuals during the course of the study. Much to my chagrin (and equal delight), researchers exceeded this goal long before the first field season came to a close. Success sparked youthful enthusiasm while experience brought a better understanding of ecological and behavioral underpinnings of the bobcat's good fortunes.

Organizing a symposium at The Wildlife Society's 7th Annual Conference was a natural extension of our interests in "Current Bobcat Research and Implications for Management." We hope these proceedings help to foster an appreciation of the bobcat by contributing to current knowledge. After all, their strategies for survival merit respect—even if they attract comparisons with a louse.

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# BOBCAT RESEARCH AND MANAGEMENT: HAVE WE MET THE CHALLENGE?

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***Abstract***: Bobcats (*Lynx rufus*) first attracted research attention for economic reasons related to predation, or their value as a furbearer. As late as 1971, bobcats were neither protected nor purposefully managed in 40 of the 48 contiguous United States. This laissez-faire attitude prevailed until the mid-1970s when attitudes toward predators changed and pelt values increased. Amid concerns that the species could be at risk, it became subject to management scrutiny and a surge of research projects. Concern for the species led to a 1979 conference at Front Royal, Virginia, where biologists presented research and shared information and insight. Papers summarized current research and management, and discussion provided ample opportunity to exchange information and viewpoints. A rapporteur noted that the species' natural history in diverse habitats was well known, but he identified serious problems and gaps in knowledge. Further, he criticized rigor of the science applied to better understand and manage bobcats and believed the information presented fell short of knowledge needed to properly manage the species throughout its range. Twenty-one years have passed and it is appropriate to meet, share our state of knowledge, and examine the purpose, approach, and rigor of bobcat research. This symposium presents bobcat research in an ecosystem context, and at spatial and temporal scales not possible 2 decades ago because our predecessors lacked the powerful tools of data acquisition and analyses we enjoy. Managers discuss challenges and their approaches to address conflicting public demands in a rapidly changing environment. We present this symposium so our audience can reflect on new knowledge, question our assumptions and methods, and help identify important questions and new approaches to improve management of bobcats and their ecosystems in the decades ahead.

***Key words***: bobcat, ecology, *Lynx rufus*, management, research.

The bobcat (*Lynx rufus*) first attracted management and research attention for economic reasons related either to its impact as a predator or its value as a furbearer. Increasing public awareness and ecological interest in native cats grew in the 1970s and led to heightened concerns for the species well being. Amid concerns that the bobcat could be at risk, it became subject to management scrutiny and prompted a surge of research projects covering a range of topics. This interest and concern led to the 1979 Bobcat Research Conference in Front Royal, Virginia, co-hosted by the National Wildlife Federation and the Endangered Species Scientific Authority. The conference was designed to provide a forum where biologists studying bobcats could present their work and share information and insight. Twenty-one years have passed and it is appropriate to again meet to share our state of knowledge and subject the purpose, approach, and rigor of bobcat research and management to peer scrutiny. The species seems to be faring well throughout its range (Woolf and Hubert 1998), but ecological understanding remains incomplete and science-based management faces new challenges in a rapidly changing landscape.

This symposium presents research on bobcats that was conducted in the context of the ecosystems they are components of, and at spatial and temporal scales not possible 2 decades ago. The research employed more powerful tools of data acquisition and analyses than were available to earlier biologists. Management issues addressed are those at the forefront of approaches used to address public concerns and conflicting demands in a rapidly changing environment. We present this symposium so our audience can reflect on our new knowledge, question our assumptions and methods, and help identify important questions and new approaches to improve science-based management of bobcats and their ecosystems.

## THE PATH TO TODAY

The bobcats extensive distribution on the North American continent attests to its versatility and adaptability. In the early history of wildlife management, especially management of predators or furbearers, there was little incentive to consider need to manage its habitats or populations. As late as 1971, bobcats were not protected nor purposefully managed in 40 of the 48 contiguous United States (Faulkner 1971). The beginnings of public awareness and concern about mammalian predators was impetus for a symposium held at the North American Wildlife and Natural Resources Conference in 1971 to review status of the native felids of North America (Jorgensen and Mech 1971). The symposium consisted of 21 presentations with a strong focus on status and management; 8 included discussions of the bobcat. In a summary of the symposium, Cowan (1971) described the bobcat as an adaptable and successful species that was the most numerous of North American felids. Further, his review of the papers presented at the symposium led Cowan (1971:6) to conclude that management was in general not regarded as necessary. This laissez-faire approach toward management prevailed until changing attitudes toward predators and a dramatic increase in pelt value during the mid- to late-1970s led to public and professional concern for the welfare of the species. This concern was magnified when the bobcat was listed in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in 1975. The listing made state management subject to federal review and agencies had to prove that harvesting bobcats was not detrimental to populations (Rolley 1987).

Additional reviews of the bobcat's status followed (Woolf and Hubert 1998), but they did not allay either public or agency concern. The continued concern led to the 1979 Front Royal, Virginia, conference that focused just on the bobcat (Escherich and Blum 1979). Whereas the 1971 symposium and other surveys (e.g., Deems and Pursley 1978) were essentially a compilation of reports on status and management, the Front Royal conference sought to provide an opportunity for researchers to present and discuss recent research and work in progress. The conference took place at a time when interest in the bobcat was high, and there were a number of new research projects underway throughout the country. Researchers presented 29 papers; some discussed status and management, but a number addressed bobcat ecology. Not everyone was impressed with the scope and substance of the research presented. A rapporteur (Dyer 1979) noted that the species natural history in diverse habitats was well known, but he identified serious problems and gaps in knowledge. Further, he criticized rigor of the science applied to better understand and manage bobcats and believed the information presented fell short of knowledge needed to properly manage the species throughout its range.

A comprehensive compilation of bobcat literature by Tumlison et al. (1985) provided evidence of increasing interest in the bobcat, and a changing focus of research beginning in the 1970s. They assembled and cross-indexed citations into 11 major topics; we selected 4 to illustrate changing emphasis of research in the 1970s and 1980s compared to prior years. The topic "food habitats and predation" included 115 citations; 53% dated before 1970. "Behavior and home range" only included 54 citations, but 69% were dated after 1970. "Ecology and population characteristics" (this topic included population dynamics, techniques for population assessment, general ecology, density, and scent-station surveys) included 91 references of which 85% were dated after 1970. The category "miscellaneous references" also illustrated the increasing interest in bobcats in the 1970s and 1980s compared to prior years; 71% of the citations were more recent than 1970.

Although different research topics were emphasized beginning in the 1970s, bobcat populations remained a source of concern for resource managers. In 1990, the bobcat again was the focus of a review of its status and management (Kulowiec 1990). Finally, the status and management of bobcats spanning the last 3 decades was reviewed by Woolf and Hubert (1998). The path we took to arrive at this symposium is one that followed changing public values, management models and emphasis, and better knowledge upon which to establish science-based management. One common thread has been concern for the well-being of the bobcat; a concern shared both by resource managers and the public they serve.

## HAVE WE MET THE CHALLENGE?

Dyer (1979) was disappointed in the science he was asked to review at the Front Royal conference that represented the knowledge of the day. Whether one judges his criticisms as perceptive and insightful or the intellectual arrogance of a person who failed to appreciate the difficulties of studying a secretive carnivore, they deserve our introspection. He thought the papers presented lacked rigor as evidenced by a tendency to ignore study objectives, failure to state approaches in terms of hypotheses, and failure to utilize the breadth of pertinent scientific literature. He noted that nothing was said about niche/competition theory, and lamented that home range was discussed, but not in context. Another troublesome criticism, if true, was his perception that tools such as radiotelemetry were used as gimmicks rather than to address strong scientific questions. There were other criticisms as well, and overall, he believed it was necessary to consider major changes in the conduct of bobcat research and management to satisfy both CITES and local issues. Finally, he took exception that the bobcat population was a central focus of the Front Royal conference and maintained there was need for more expansive thinking and use of community and ecosystem function paradigms as the backbone leading to management strategies (Dyer 1979:135–136).

What would he say today if asked to summarize these proceedings? Few could have imagined the new tools now at our disposal and how computers, radiotelemetry, and remote sensing have combined to offer insight about bobcat ecology simply not possible 2 decades ago. Good science always begins with asking an important question, but without doubt, the tools now at our disposal have allowed such questions to be addressed as evidenced by the research presented at this symposium.

However, the real issue is the quality and rigor of our science; are the criticisms posed 21 years ago still an issue today? We believe the papers in this symposium are of a quality that can withstand critical peer evaluation. Hypotheses are in evidence, and most papers reflect studies of bobcats in context of the ecosystems they occupy, and at temporal and spatial scales previously unimaginable. Both niche and competition theory are addressed, and there is now meshing of theoretical and empirical approaches that Dyer (1979:135) found lacking. Perhaps most importantly, our powerful new tools have allowed insights into species-habitat relationships that offer promise of habitat-based management decisions not even envisioned 2 decades ago.

The single species approach persists, but is this really a valid criticism or concern? We do not apologize for featuring the bobcat, because in truth, the research presented has focused on the species in an ecosystem context. Managers also focus on the species, but that is their charge. However, they too understand that the bobcat does not live in isolation, and their management decisions are increasingly habitat-based and cognizant of landscape-level scales.

## A GLIMPSE AT TOMORROW

Those who will be charged with managing the bobcat in the future will start from a position of strength. By most accounts, the continental bobcat population is healthy (Woolf and Hubert 1998) and fears for its future well-being, professed in the 1970s, were unfounded. Bobcats were delisted as state threatened in Illinois in 1999 (Bluett et al. 2001), and in Pennsylvania, the Game Commission (Lovallo 2001) approved a legal harvest of bobcats for the first time in 30 years. Further, managers and their management strategies have adapted to changing times and needs. Better data are available upon which to implement science-based management, and agencies are making harvest management decisions on that basis capable of withstanding legal challenges (Rolley et al. 2001).

However, managers most likely will face more difficult issues to resolve, and the need for scientifically sound information upon which to formulate and defend management options will increase. Adverse impacts of humans and their activities on wildlife and their habitats also can only increase. Bobcats seem tolerant of human presence, but exurban development will intensify pressure on bobcat populations (Nielsen and Woolf 2001). Finally, public policy already shapes management decisions, but increasingly, human dimensions aspects will outweigh ecological considerations when formulating management strategies (Bluett et al. 2001).

In spite of increasing human pressure and increasingly contentious debates over management goals and objectives, we remain optimistic. The bobcat indeed is an adaptable species as Cowan (1971) noted long ago. Also, wildlife managers and researchers have always been up to challenges posed. We predict that both bobcats and those who manage them will prevail and we hope this symposium contributes to that outcome.

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# MULTIVARIATE MODELS OF BOBCAT HABITAT SELECTION FOR PENNSYLVANIA LANDSCAPES

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***Abstract***: We used bobcat (*Lynx rufus*) locations, a geographic information system, multivariate statistical modeling techniques, and remotely sensed land cover and physiographic data to model bobcat habitat selection and to predict distribution of suitable habitat in Pennsylvania. Bobcats (27 F, 34 M) were radiocollared and monitored on a 2,320-km$^2$ study area during 1986–97. We developed Mahalanobis distance-based models of habitat selection on the study area and used logistic regression techniques to extrapolate patterns of habitat selection to larger scales. The models classified 70% and 54% of the study area as suitable for males and females, respectively. Cross-validation suggested 86% classification success for both males and females. The model was validated using independent locations collected from 7 female and 10 male bobcats. Validation suggested 78% classification success for females and 71% success for males. Female home range size was inversely correlated ($r = -0.67$, $P = 0.004$) with percent composition of areas classified as suitable habitat suggesting model predictions reflected habitat gradients that were linked to individual behavior and home range use. An area of 18,564 km$^2$ (15.8% of Pennsylvania) was classified as suitable for both male and female bobcats, whereas 39,067 km$^2$ (33.3%) was suitable for males but not females. Our results provide an information source for habitat-based management decisions and serve as a basis for hypotheses addressing local- and landscape-level habitat associations.

***Key words***: bobcat, distribution, habitat modeling, geographic information systems, logistic regression, *Lynx rufus*, Mahalanobis distance, multivariate statistics.

The use of quantitative habitat models and geographic information systems (GIS) in wildlife science is rapidly increasing for resource inventory, impact assessment, mitigation, and the development of wildlife management objectives (Schamberger and ONeil 1986). Habitat models are usually developed from field investigations of species-habitat relationships and then extrapolated to evaluate habitat conditions in other regions. These models are often developed on a site-specific basis and are rarely validated beyond the geographic extent of their development (Lancia et al. 1982). Current interest by state and federal agencies in predicting the spatial occurrence of suitable habitats, as evidenced by the Gap Analysis Program (Scott et al. 1993), illustrates the need to make better use of site- and species-specific habitat relationship models in predicting broad-scale spatial distributions of animal species.

The geographic range of the bobcat includes most of the contiguous U.S., with the exception of major agricultural regions of the Midwest and Mexico (Anderson 1987, Boyle and Fendley 1987). Bobcat populations in Pennsylvania are established throughout the northern, central, and southcentral portions of the state (Giles 1986, Merritt 1987, Lovallo 1999) and provide an important geographic link between established populations in New York to those of the southeastern U.S. The bobcat was first classified as a game animal in Pennsylvania in 1970, which empowered the Pennsylvania Game Commission (PGC) to set regulations to manage bobcat populations. Before 1970, bobcats were unprotected in Pennsylvania and bounties were paid during 1819–1937 (Giles 1986). Recent surveys of PGC field personnel and sportsmen suggest the geographic range of the bobcat is expanding and that bobcat density has increased since the 1970 reclassification (Lovallo 1999).

The development of effective management strategies for Pennsylvania bobcats requires a fundamental understanding of bobcat-habitat relationships as they relate to abundance and distribution. The PGC is currently developing a habitat-based management plan for bobcats (Lovallo 2001). The development and implementation of this plan requires an understanding of bobcat habitat selection and a statewide assessment of the amount and distribution of suitable bobcat habitat. Despite a proliferation of field investigations on bobcat habitat selection during the late 1970s and early 1980s (Anderson 1987), there are no published reports of bobcat habitat selection in Pennsylvania.

We estimated bobcat habitat selection in northcentral Pennsylvania and used multivariate habitat modeling to predict the extent and distribution of suitable bobcat habitat. We compared models using Mahalanobis distance measures based on spectral reflectance and physiographic characteristics to logistic regression models based on classified satellite imagery and physiographic characteristics. We evaluated model performance using cross-validation techniques and an independent sample collected beyond the geographic extent of model development. We also described the extent and distribution of suitable bobcat habitat using cell-by-cell, sex-specific, predictions of habitat suitability, and compared amounts of suitable habitat within bobcat home ranges to habitat composition within simulated bobcat home ranges statewide.

## STUDY AREA

Field investigations were conducted in a 2,320-km$^2$ study area (hereafter, Study Area 1) in northern Lycoming County, Pennsylvania. The study area was located in the Allegheny Plateau province and was underlain with Devonian and Mississippian bedrock. The area was characterized by steep, forested slopes and narrow drainages. Soils were primarily incepticols originating from glacial till. The study area was primarily forested with active agriculture in the lower elevations. Forests were dominated by northern hardwood types including sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*), and hemlock (*Tsuga canadensis*). Other prevalent species included white pine (*Pinus strobus*), basswood (*Tilia americana*), mountain laurel (*Kalmia latifolia*), and American ash (*Fraxinus americana*).

## METHODS

### Capture, Marking, and Monitoring

Bobcats were captured in offset #1.75 coilspring traps by trappers and PGC employees during 1986–95. Bobcats were immobilized with ketamine hydrochloride and equipped with radiocollars and numbered eartags. All bobcats were released immediately following capture. Initial efforts to capture bobcats during 1986–93 were focused on Study Area 1, whereas subsequent capture efforts (1993–95) were expanded to include areas within 150 km of Study Area 1 (hereafter, Study Area 2).

Bobcats were located using fixed-wing aircraft (Mech 1983) and ground-based triangulation using 2-element H-style antennas. Aerial-determined locations were periodically ground-truthed by PGC employees to verify telemetry accuracy. Bobcat locations were grouped by sex and season (sum: 15 May–31 Aug, win: 1 Oct–14 May). Seasonal designations were chosen based on the reproductive biology of bobcats. The summer period encompassed parturition and kitten rearing periods for females, whereas the winter period included the breeding season.

### Habitat Variables

Measures of elevation, aspect, and slope were based on digital, statewide data derived from 2-arc-second (30 min), United States Geological Survey digital elevation models. Digital elevation models were produced via interpolation of digital line graph hypsographic and hydrographic data and had an associated root-mean-square-error of 0.5 contour intervals. A GIS (ARCINFO; ESRI, Redlands, California, USA) was used to resample digital elevation models into 30-m lattices and to interpolate elevation (m), aspect (degree of exposure), and slope (degrees) measures associated with bobcat locations. Spectral reflectance data (30x30-m resolution) were obtained from Landsat Thematic Mapper sensors during May 1993. A 31,470-km$^2$ scene that encompassed northcentral Pennsylvania was used to assign 6 bands of reflectance data to bobcat locations.

Univariate analyses of habitat selection and logistic regression models were based on classified land cover data and considered 7 land cover categories: coniferous forest, mixed forest, broadleaf forest, transitional areas, perennial herbaceous, annual herbaceous, and unvegetated areas. Land cover data were generalized to 1-ha resolution and stored at 30x30-m resolution as part of Pennsylvanias contribution to the National Gap Analysis Project (W. Myers, The Pennsylvania State University, unpublished data; Scott et al. 1993).

### Univariate Habitat Selection

Univariate analyses of cover type selection were based on the actual use of cover types compared to their expected use based on proportional occurrence within Study Area 1 (Neu et al. 1974). Because sufficient numbers of locations were not available to test for habitat selection by individual bobcats, locations were pooled across individuals and habitat selection was estimated separately for males and females each during the summer and winter seasons. Availability of cover types was based on a minimum perimeter convex polygon estimated from all bobcat locations. Bonferroni $z$-tests were used to construct 95% confidence intervals to identify selection or avoidance of particular types. Chi-square contingency tests were used to compare habitat use between sexes and seasons (Zar 1984).

We used a modified goodness-of-fit to test for circular uniformity among aspect measures associated with male and female bobcat locations during summer and winter. This test is insensitive to the starting point of a circle and is widely applied to circular data (Batschelet 1965). Standard deviations for aspect measures were calculated according to Mardia (1972). Rayleigh's $z$-test was used to test for a mean aspect when distributions were unimodal (Zar 1984). Kuiper Chi-square tests of heterogeneity were used to compare aspect measures between seasons and sexes (Zar 1984).

### Home Range Estimates

We used 3 independent methods, including the adaptive kernel estimator (Worton 1989), harmonic mean estimator (Dixon and Chapman 1980), and minimum convex polygon technique (Mohr 1947), to estimate annual home range size for male and female bobcats. Because sample size was limited for some individuals, only annual ranges were constructed. All home range methods used 95% probability distributions. We used program CALHOME (Kie et al. 1996) to estimate home range size and to export resulting polygons to a GIS. We used a Wilk-Shapiro test to assess normality of home range estimates.

**Habitat Modeling**

We used 2 independent approaches and a combined approach to model bobcat habitat selection within Study Area 1. The first approach used Mahalanobis distances as measures of habitat similarity and considered 8 variables including 6 measures of spectral reflectance, slope (degree change), and aspect (circular measure of exposure in degrees). The second approach was based on logistic regression that evaluated cover type, slope, and aspect measured at bobcat locations relative to habitat conditions at random locations within the study area. The combined approach also used logistic regression and compared used versus random locations. However, only random locations that occurred in areas classified as unsuitable, based on the Mahalanobis distance-based model, were used in the regression. Hereafter, we refer to this randomization scheme as "conditional."

*Mahalanobis Distance Mode.*—We developed a multivariate habitat selection model based on Mahalanobis distances that was similar to Clark et al. (1993). This model was fundamentally based on the use of Mahalanobis distance as a relative measure of habitat similarity. Mahalanobis distance calculations were used to assign various levels of habitat suitability for female and male bobcats on a cell-by-cell basis (Seber 1984). This procedure used the covariance matrix from each set of locations to produce a multi-space transformation in which distance between the reflectance, aspect, and slope of a geographic cell and the mean reflectance, aspect, and slope associated with radiolocations represented an index to habitat similarity. Kolmogorov-Smirnoff tests were used to determine distributions that best fit sample distances in Mahalanobis space (Zar 1984). Geographic cells were classified as selected habitat if they fell within the upper 90% of the distribution associated with a given sex. Our methods differed from Clark et al. (1993) in 2 respects: (1) models were developed independently for males and females to assess intersexual variation in habitat selection and to identify sex-specific patterns in habitat distribution, and (2) habitat models were developed, in part, from direct spectral reflectance rather than from classified land cover types.

*Logistic Regression Models.*—Logistic regression models of habitat suitability were developed according to the approach outlined by Hosmer and Lemeshow (1989). Logistic regression models were developed as the logit of probability of presence as a linear function of categorical and continuous regressor variables. Logistic regression models were based on habitat conditions associated with cells classified as used, based on the occurrence of bobcat locations ($n = 804$ for M; $n = 1{,}518$ for F), and at randomly selected cells within the study area. These models considered the 7 cover-type variables, slope, and aspect. Aspect was represented as 4 categorical variables, each encompassing 90° intervals. The first aspect variable, Aspect(I), was centered on the estimate of the circular mean and consecutive aspect intervals (i.e., Aspect(II), Aspect(III), and Aspect(IV)) were assigned clockwise. We fit univariate logistic regression models and examined likelihood ratio tests to determine inclusion in multiple logistic regression models.

We used 2 approaches to select random points for the development of logistic regression models: a completely random approach and a conditional random approach. The completely random approach used all randomly selected points ($n = 2{,}893$) within the study area boundary. The conditional random approach used only randomly selected points believed to be located in poor habitat ($P \leq 0.10$) based on sex-specific, Mahalanobis distance-based models of habitat selection ($n = 804$ for M, $n = 1{,}518$ for F). Random coordinates were generated using algorithms described by Press et al. (1992).

We examined relationships between home range size and percent composition of suitable habitat, as determined from Mahalanobis distance and logistic regression models, to determine whether distribution and amounts of suitable habitat affected home range size. Home range boundaries were overlaid onto maps of predicted habitat suitability and the percent composition of suitable habitat in each range was determined. We hypothesized that home range size would be inversely related to the percent composition of suitable habitat within the home range and that the magnitude of inverse correlations would relate various levels of habitat suitability.

**Model Validation**

Bobcat habitat selection models were validated at 2 scales: within Study Area 1, and regionally throughout northcentral Pennsylvania. Within the study area, jackknife cross-validation techniques were used to estimate reclassification success using the initial set of bobcat locations (Lachenbruch and Mickey 1968). In the case of Mahalanobis distance-based models, we compared the actual habitat components (i.e., cover type, slope, aspect) associated with patches classified as suitable habitat to results from univariate habitat selection analyses.

At the regional level, habitat selection models were applied to areas occupied by bobcats radiocollared in Study Area 2. Locations ($n = 158$ for F, $n = 200$ for M) were attributed by predicted bobcat suitability scores and classification success rates were calculated.

**Statewide Model Application**

Regional validation results were used to determine which modeling approach would perform best for statewide extrapolation. We used existing statewide geographic data including slope, aspect, and classified land cover to make cell-by-cell (30x30-m resolution), sex-specific predictions of bobcat habitat suitability. We estimated amounts of suitable male and female bobcat habitat within counties, furbearer management zones, and

Wildlife Conservation Officer (WCO) districts to provide a geographic basis for future refinement of bobcat management zones.

**Home Range Size Versus Habitat Predictions**

We used estimates of percent composition of suitable habitat within actual female home ranges and a moving window approach to evaluate potentials of simulated home ranges throughout Pennsylvania to support female bobcats. Although habitat selection models were developed for males and females, we based the statewide analyses of home range potential only on females because females generally use higher quality habitat than males (Bailey 1974), and female home range size is directly related to habitat quality whereas male home range size may be influenced by breeding opportunities (e.g., the spacing pattern of females) (Anderson 1987). We developed circular home ranges of approximately the same area as median female home range sizes observed in our study. These simulated home ranges were developed statewide and served as the spatial units for comparison to actual home range characteristics. Home range centers were spaced at 2,500-m horizontal and vertical intervals. We used this sampling strategy to identify fine-scale gradients in the potential of simulated home ranges to support female bobcats and to negate random effects due to the placement of simulated ranges.

**Statewide Model Validation**

We used a questionnaire to survey WCOs concerning their perceptions on the distribution and status of bobcat populations within their respective districts. In most cases, the 67 counties in Pennsylvania are patrolled by 2 or 3 WCOs; each is assigned to 1 of 138 districts in the state. In districts where WCOs were relatively new, we requested that advice be sought from the previous WCO or from WCOs in surrounding districts. Survey results were compared to the predicted habitat composition of each district.

Existing information on reported bobcat mortalities was also used to identify bobcat presence/absence within counties. Pennsylvania Game Commission staff collected reports of bobcat mortalities during 1986–99. Recovered bobcats were weighed and sex and age (juv vs. ad) were determined. Date of death, cause of death (if possible), and location were recorded by county and township. A spatial data layer containing county boundaries was attributed by numbers of bobcat mortalities and was compared to the statewide distribution of suitable habitat.

## RESULTS

**Capture, Marking, and Monitoring**

Sixty-one bobcats (27 F, 34 M) were captured and radiocollared in northcentral Pennsylvania during 1986–95. Initial efforts to model habitat suitability were based on radiolocations collected from 20 females and 24 males on Study Area 1. Extrapolation beyond Study Area 1 was evaluated using locations collected from 7 females and 10 male bobcats captured and radiocollared on Study Area 2 during 1993–95.

**Univariate Habitat Selection**

Slope measures associated with bobcat locations revealed differences by sex ($F_{3,2318} = 44.71$, $P < 0.001$) and season ($F_{3,2318} = 5.74$, $P = 0.017$). Females spent more time on steeper slopes during winter ($\bar{x} = 8.2°$, SE = 0.2) than during summer ($\bar{x} = 7.3°$, SE = 0.3). Regardless of season, males used steeper slopes than females ($\bar{x} = 8.4°$, SE = 0.2 during winter; $\bar{x} = 8.3°$, SE = 0.5 during summer). Comparison of aspect measures associated with bobcat locations revealed circular non-uniform distributions for both males and females during summer and winter periods. Plotting aspect measures by 30° intervals suggested distributions were unimodal and mean angles and circular standard deviations could be calculated. Aspect measures associated with bobcat locations differed between males and females regardless of season. Females were most often located on eastern aspects, whereas males were associated with eastern aspects during summer and southeastern aspects during winter (Fig. 1).

Female bobcats did not use cover types in proportion to their availability ($\chi^2_6 = 35.62$, $P < 0.001$ during summer; $\chi^2_6 = 55.71$, $P < 0.001$ during winter) (Table 1). Females selected broadleaf deciduous forests and avoided herbaceous and unvegetated areas during summer and winter. There was no seasonal difference in habitat selection for females ($\chi^2_6 = 10.62$, $P = 0.060$). Males also used cover types disproportionately to their availability ($\chi^2_6 = 42.13$, $P < 0.001$ during winter; $\chi^2_6 = 12.15$, $P < 0.001$ during summer) (Table 1). Male bobcats selected broadleaf deciduous forest during summer and winter. Males avoided conifer forests and annual herbaceous areas during summer and avoided mixed forest, unvegetated areas, and perennial herbaceous areas during winter. There was no seasonal difference in cover type selection for males ($\chi^2_6 = 3.57$, $P = 0.140$).

**Home Range Estimates**

We only used home ranges estimated from ≥20 locations in the analyses. Home ranges were calculated for 17 of 34 males and 17 of 26 females (Table 2). Home range size was non-normal ($P < 0.01$) for males and females, regardless of the estimator used. Median male home ranges were 2.5, 2.8, and 4.8 times greater than those of females based on minimum convex polygon, harmonic mean, and adaptive kernel estimators, respectively. Median home ranges and associated quartiles were similar between minimum convex polygon and harmonic mean estimators, whereas home ranges estimated using the adaptive kernel method were approximately twice as large as those estimated by other methods.

**Habitat Modeling**

*Mahalanobis Distance Model.*—Mahalanobis distance-based models classified 69.6% of the initial study area as suitable ($P \geq 0.10$) for males and 54.0% suitable ($P > 0.10$) for females (Fig. 2). Suitable habitat areas were dominated by forest cover types (approximately 85% and 95% for M and F, respectively). Percent composition of conifer and mixed cover types in suitable

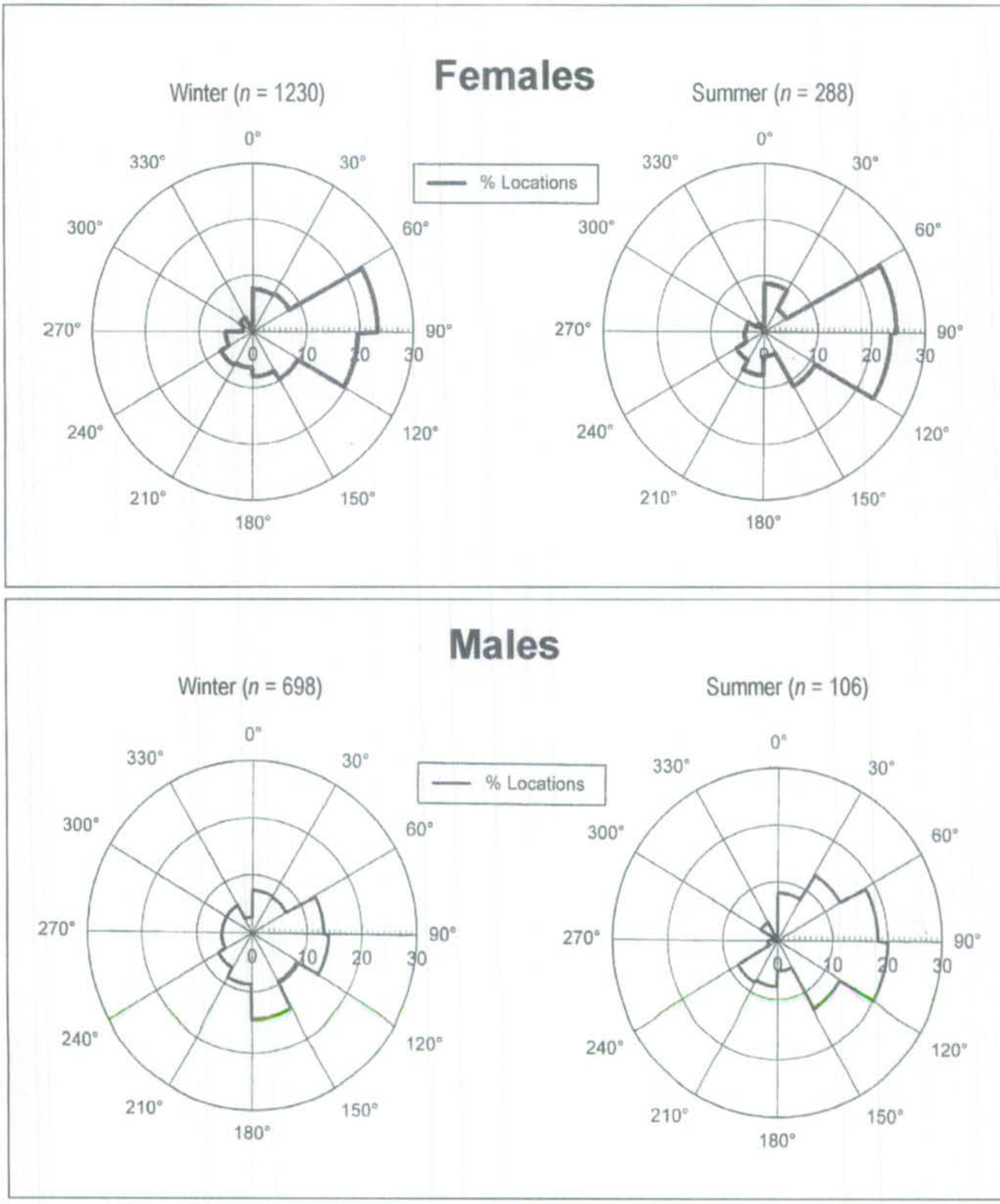


Fig. 1. Circular distributions of aspect measures associated with male and female bobcat locations in northcentral Pennsylvania during 1986–93.

patches gradually decreased as habitat suitability increased. Percent composition of broadleaf deciduous forest in suitable patches remained relatively constant and high in the most suitable habitats. Areas classified as unsuitable ($P < 0.10$) contained a mix of cover types including several types avoided by bobcats as indicated by univariate measures of cover type selection (e.g., unvegetated and herbaceous areas).

As habitat suitability increased, aspect associations within patches classified as suitable habitat approached the average measures for both males and females, as determined from univariate tests of aspect measures. The measure of circular uniformity of aspect measures ($r$) decreased at a constant rate as suitability ranged from 0 to 1.0 and became very directional at high suitability scores. Average slopes in high suitability areas approached mean values associated with bobcat locations.

Mahalanobis distance-based habitat suitability models identified 49% of forested areas as suitable for both male and female bobcats; 40% of these areas were composed of broadleaf deciduous forest. However, not all stands of broadleaf deciduous forest were identified as suitable. Nineteen percent of broadleaf deciduous forest was classified as unsuitable for males and females due to unfavorable slope and aspect conditions. Male habitat suitability models identified an additional 10% of broadleaf deciduous forest type and 3% of mixed forest type that were not suitable for females. Conversely, only a very small proportion (0.2%) was identified as suitable for females but not for males.

*Logistic Regression Model (Complete Randomization)*.—Evaluation of univariate logistic regression models resulted in the elimination of 3 variables for males (coniferous forest, transitional areas, and Aspect[IV]). Broadleaf deciduous forest, slope, Aspect(I), and Aspect(IV) had significant positive parameter estimates. All other parameter estimates were negative. Evaluation of parameter estimates in the multiple logistic model resulted in the elimination of mixed forest and annual herbaceous types. Broadleaf deciduous forest, slope, and

Table 1. Cover type selection by bobcats based on radiolocations in northcentral Pennsylvania during 1986–93.

| | | Summer | | | | Winter | | | |
|---|---|---|---|---|---|---|---|---|---|
| Cover type | Prop. of study area | $n$ | $P_i$ | 95% CI ($P_i$) | Preference | $n$ | $P_i$ | 95% CI ($P_i$) | Preference |
| Females | | | | | | | | | |
| Conifer forest | 0.015 | 9 | 0.031 | (0.003–0.058) | - | 17 | 0.014 | (0.005–0.023) | - |
| Mixed forest | 0.159 | 32 | 0.111 | (0.061–0.161) | - | 176 | 0.143 | (0.116–0.170) | - |
| Broadleaf forest | 0.698 | 226 | 0.785 | (0.720–0.850) | Selected | 940 | 0.764 | (0.732–0.797) | Selected |
| Transitional vegetation | 0.045 | 19 | 0.066 | (0.027–0.105) | - | 62 | 0.050 | (0.034–0.067) | - |
| Perennial herbaceous | 0.031 | 1 | 0.003 | (0.000–0.013) | Avoided | 15 | 0.012 | (0.004–0.021) | Avoided |
| Annual herbaceous | 0.027 | 1 | 0.003 | (0.000–0.013) | Avoided | 16 | 0.013 | (0.004–0.022) | Avoided |
| Unvegetated | 0.022 | 0 | - | - | Avoided | 4 | 0.003 | (0.000–0.008) | Avoided |
| Males | | | | | | | | | |
| Conifer forest | 0.015 | 0 | - | - | Avoided | 7 | 0.010 | (0.000–0.020) | - |
| Mixed forest | 0.159 | 12 | 0.113 | (0.030–0.196) | - | 84 | 0.122 | (0.089–0.156) | Avoided |
| Broadleaf forest | 0.698 | 89 | 0.840 | (0.744–0.935) | Selected | 548 | 0.797 | (0.755–0.837) | Selected |
| Transitional vegetation | 0.045 | 3 | 0.028 | (0.000–0.072) | - | 28 | 0.041 | (0.020–0.061) | - |
| Perennial herbaceous | 0.031 | 1 | 0.009 | (0.000–0.035) | - | 6 | 0.009 | (0.000–0.018) | Avoided |
| Annual herbaceous | 0.027 | 0 | - | - | Avoided | 12 | 0.017 | (0.004–0.031) | - |
| Unvegetated | 0.022 | 1 | 0.009 | (0.000–0.035) | - | 3 | 0.004 | (0.000–0.011) | Avoided |

Table 2. Home range sizes ($km^2$) of bobcats in northcentral Pennsylvania during 1986–93 using adaptive kernel, harmonic mean, and minimum convex polygon (MCP) methods. Only home ranges based on >20 radiolocations were used for analysis.

| | Males ($n$ = 17) | | | | Females ($n$ = 17) | | | |
|---|---|---|---|---|---|---|---|---|
| Method | Norm.[a] R ($P$) | Med. | Range | Q1 - Q3 | Norm.[a] R ($P$) | Med. | Range | Q1 - Q3 |
| Adaptive kernel | 0.78 (<0.01) | 114.5 | 14.3–1,048.0 | 25.3–229.5 | 0.78 (<0.01) | 23.5 | 3.3–442.3 | 15.6–71.8 |
| Harmonic mean | 0.72 (<0.01) | 44.4 | 7.7–625.1 | 13.1–86.1 | 0.85 (<0.01) | 16.1 | 2.2–179.2 | 11.0–52.2 |
| MCP | 0.82 (<0.01) | 42.2 | 7.2–430.6 | 15.7–102.6 | 0.81 (<0.01) | 17.2 | 2.8–169.8 | 10.3–35.8 |

[a]Shapiro and Wilk test for normality. Small $P$-values indicate a non-normal distribution.

Aspect(I) had positive parameter estimates, suggesting favorable contributions to habitat suitability. Unvegetated areas, perennial herbaceous areas, and Aspect(III) had negative parameter estimates with unvegetated areas providing the greatest influence (Table 3).

Evaluation of univariate logistic regression models for females resulted in the elimination of transitional areas. Broadleaf deciduous forest, slope, and Aspect(I) had significant positive parameter estimates; all other parameter estimates were negative. Evaluation of parameter estimates in the multiple logistic model led to the elimination of Aspect(IV). All forest types (conifer, mixed, and broadleaf deciduous), slope, and Aspect(I) had positive parameter estimates suggesting favorable contribution to bobcat presence. Herbaceous areas, unvegetated areas, Aspect(II), and Aspect(III) had negative parameter estimates (Table 3).

*Logistic Regression Model (Conditional Randomization)*.—Evaluation of univariate logistic regression models resulted in the elimination of 3 variables for males (coniferous forest, transitional areas, and Aspect[II]). Broadleaf deciduous forest, slope, Aspect(I), and Aspect(IV) had significant positive parameter estimates. All other parameter estimates were negative. Evaluation of parameter estimates in the multiple logistic model led to the elimination of mixed forest. Broadleaf forest, slope, and Aspect(I) retained positive parameter estimates suggesting favorable conditions for bobcat presence. Unvegetated areas, herbaceous areas, and Aspect(III) had negative parameter estimates with unvegetated areas providing the greatest influence (Table 3).

Evaluation of univariate logistic regression models suggested the elimination of 3 variables for females (transitional areas, slope, and Aspect[IV]). Broadleaf forest, slope, Aspect(I), and Aspect(IV) had significant positive parameter estimates; all other parameter estimates were negative. A multiple logistic regression model was developed from the remaining variables. Evaluation of parameter estimates in the multiple logistic model resulted in the elimination of Aspect(II). All other variables were retained in the final model. All forest types (coniferous, mixed, and broadleaf deciduous) and Aspect(I) had positive parameter estimates suggesting a favorable effect on habitat suitability. All herbaceous areas, unvegetated areas, and Aspect(III) had negative parameter estimates (Table 3).

Logistic regression models developed using conditional randomization identified 46% of the region as suitable for males and 25% as suitable for females. Fifty-one percent of the region was classified as unsuitable for either male or female bobcats. The majority of areas classified as unsuitable consisted of the broadleaf deciduous cover type. All herbaceous and unvegetated areas were classified as unsuitable habitat for both males and females.

Ninety-seven percent of all areas classified as

Table 3. Parameter estimates and significance tests from multiple logistic regression models of bobcat habitat suitability in northcentral Pennsylvania based on used versus random points. Random points were selected using complete and conditional approaches.[a]

| Males | | | | | Females | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | Parameter estimate | SE | Wald $X^2$ | $P$ | Variable | Parameter estimate | SE | Wald $X^2$ | $P$ |
| Complete randomization | | | | | | | | | |
| Broadleaf forest | 0.3874 | 0.101 | 14.629 | 0.000 | Mixed forest | 0.2251 | 0.155 | 2.1139 | 0.146 |
| Perennial herb. | -0.9876 | 0.404 | 5.983 | 0.014 | Broadleaf forest | 0.2149 | 0.131 | 2.7083 | 0.100 |
| Unvegetated | -1.1875 | 0.524 | 5.137 | 0.023 | Perennial herb. | -0.1085 | 0.303 | 11.0870 | 0.000 |
| Slope | 0.0300 | 0.005 | 27.714 | 0.000 | Annual herb. | -0.5842 | 0.302 | 3.7414 | 0.053 |
| Aspect I | 0.1309 | 0.112 | 1.357 | 0.244 | Unvegetated | -2.0921 | 0.534 | 15.3564 | 0.000 |
| Aspect II | -0.2838 | 0.118 | 5.766 | 0.016 | Slope | 0.0156 | 0.005 | 9.0224 | 0.003 |
| Aspect III | 0.5508 | 0.135 | 16.707 | 0.000 | Aspect I | 0.8411 | 0.096 | 77.0540 | 0.000 |
| | | | | | Aspect II | -0.1813 | 0.104 | 3.0131 | 0.083 |
| | | | | | Aspect III | -0.6055 | 0.120 | 25.4900 | 0.000 |
| Conditional randomization | | | | | | | | | |
| INTERCEPT | -0.3209 | 0.226 | 2.010 | 0.156 | INTERCEPT | -0.4713 | 0.204 | 5.3658 | 0.021 |
| Broadleaf forest | 0.5693 | 0.214 | 7.063 | 0.008 | Conifer forest | 1.4462 | 0.400 | 13.0827 | 0.000 |
| Perennial herb. | -1.8645 | 0.455 | 16.803 | 0.000 | Mixed forest | 0.8025 | 0.212 | 14.3979 | 0.000 |
| Annual herb. | -1.2450 | 0.387 | 10.328 | 0.001 | Broadleaf forest | 0.6809 | 0.183 | 13.8810 | 0.000 |
| Unvegetated | -2.4040 | 0.563 | 18.251 | 0.000 | Perennial herb. | -1.1137 | 0.343 | 10.5328 | 0.001 |
| Slope | 0.0090 | 0.007 | 1.703 | 0.192 | Annual herb. | -0.9542 | 0.340 | 7.8981 | 0.005 |
| Aspect I | 0.5210 | 0.143 | 13.214 | 0.000 | Unvegetated | -2.8180 | 0.552 | 26.0841 | 0.000 |
| Aspect III | -0.7790 | 0.156 | 24.800 | 0.000 | Aspect I | 1.1860 | 0.127 | 86.6519 | 0.000 |
| Aspect IV | 0.2175 | 0.160 | 1.850 | 0.174 | Aspect III | -1.1929 | 0.137 | 75.8411 | 0.000 |

[a]Random points were selected in areas classified as unsuitable based on spectral Mahalanobis distance models.

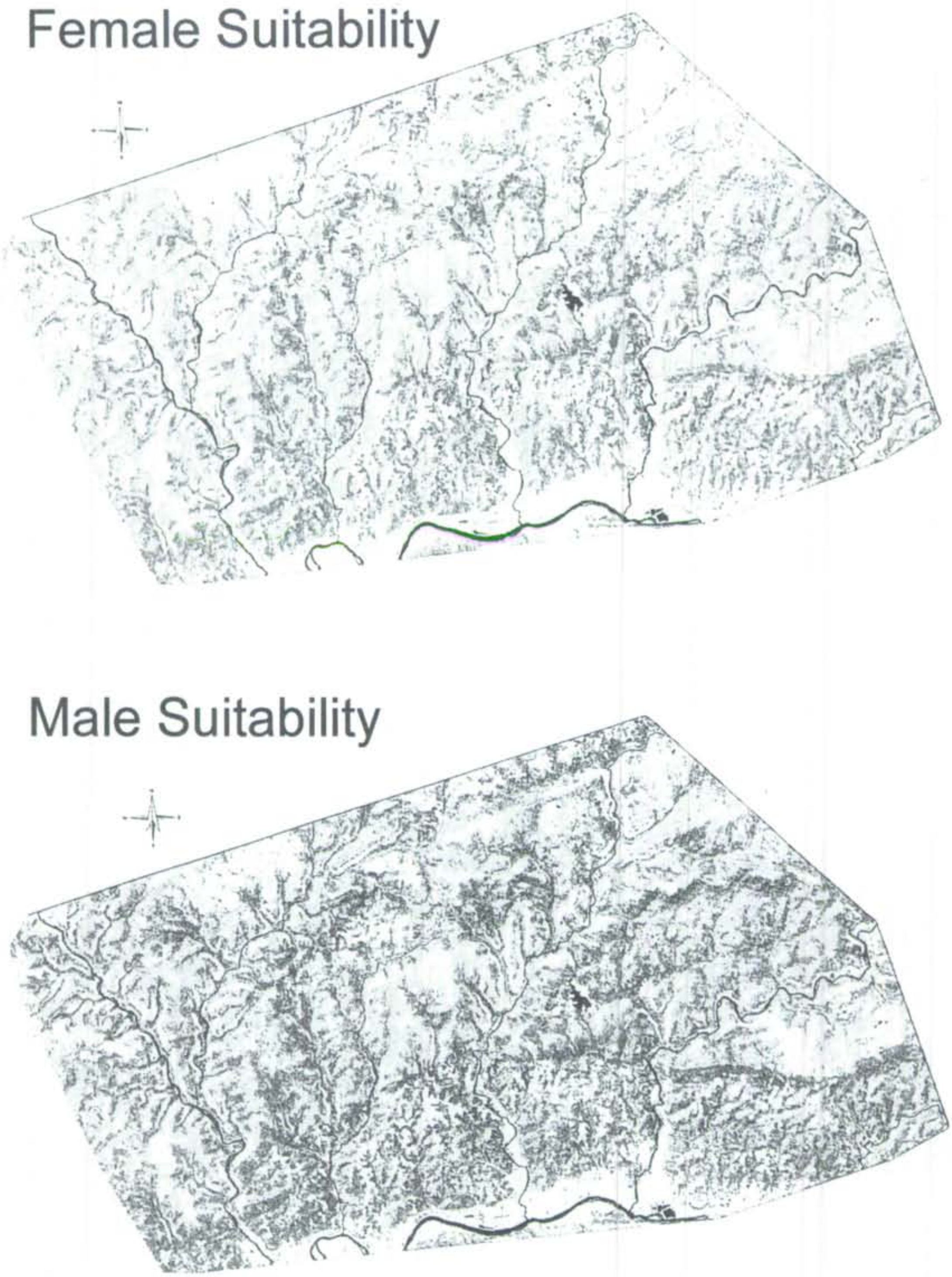


Fig. 2. Bobcat habitat suitability for males and females within Study Area 1 as predicted by Mahalanobis distance-based models using standardized spectral reflectance, aspect, and slope. All areas with $P > 0.10$ (light gray) were considered suitable habitat, whereas areas with $P > 0.50$ (dark) were considered highly suitable.

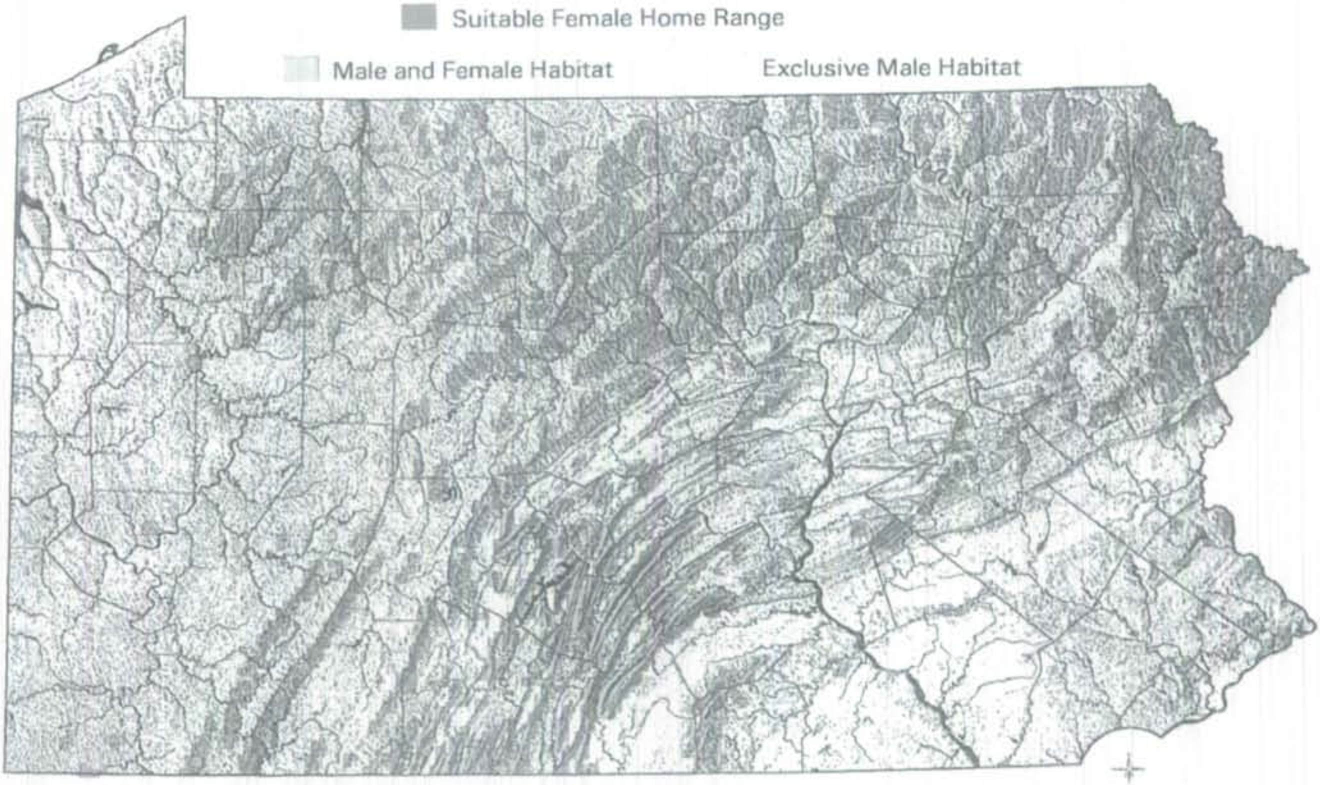


Fig. 3. Statewide distribution of suitable male and female bobcat habitat and potential female home ranges, as predicted from logistic regression models based on cover type, slope, and aspect.

suitable for females were also classified as suitable for males; whereas, 23% of the region was classified as suitable for males but not for females. The majority of areas classified as suitable for males but not for females consisted of broadleaf deciduous habitats. Small amounts (0.6–1.6% of the region) of exclusive female habitats were identified in mixed and coniferous forest and transitional cover types.

**Home Range Size Versus Habitat Predictions**

We detected significant relationships between bobcat home range size and the amount of suitable habitat within home ranges as predicted by Mahalanobis distance models. Bobcat home range size was negatively correlated ($r = -0.39$, $P = 0.057$) with percent composition of areas classified as suitable. This inverse relationship became increasingly significant as the home range composition of higher suitability levels was examined. For example, the relationship between home range size and percent composition of areas with $P \geq 0.20$ was $r = -0.44$ ($P = 0.031$), and the relationship for $P \geq 0.50$ was $r = -0.48$ ($P = 0.019$).

We observed similar relationships between home range size and the amount of suitable habitat as predicted by logistic regression models using conditional randomization. Home range size was inversely correlated to the amount of habitat classified as $P \geq 0.60$, particularly for females ($r = -0.67$, $P = 0.004$). Suitable habitat of $P > 0.60$ ranged from 17.9–46.4% within female home ranges. Home range size of females with <25% composition of suitable habitat were large and variable (e.g., 3 F with <25% composition of suitable habitat occupied home ranges >120 km$^2$). As was the case with Mahalanobis distance-based models, inverse relationships between home range size and habitat predictions became increasingly significant as the home range composition of higher suitability levels was examined.

**Validating Habitat Models**

*Cross-validation (Study Area-specific).*—Within Study Area 1, jackknife cross-validation techniques reclassified 85.7% of male bobcat locations as occurring in areas classified as suitable habitat by Mahalanobis distance models. Similarly, 86.4% of female locations were located in areas classified as suitable habitat. Disproportionately more locations were in areas of relatively high suitability ($P > 0.50$) than expected based on percent composition of Study Area 1. For example, 82% of male locations were reclassified as occurring in areas with $P \geq 0.50$, whereas only 24.6% of Study Area 1 was classified as $P \geq 0.50$. Similarly, 57% of female locations were classified as occurring in suitable areas whereas these areas only composed 14.9% of Study Area 1.

Jackknife cross-validation of logistic regression models using the complete randomization scheme indicated a classification success rate of 58% for males and 65% for females. This low classification success was largely due to a large false negative classification error (i.e., classifying bobcat locations as unsuitable). Use of conditional random points in the logistic regression models improved overall classification rates by 6.3% for males and by 3.1% for females (68.1% correct for F and 64.3% correct for M). Use of conditional randomization reduced false negative classification rates by 33% for males and 27% for females.

*Regional Validation*.—Eighty-eight percent of female locations were classified as suitable habitat by Mahalanobis distance-based models, whereas only 72% of male locations were classified as suitable. Approximately 10% fewer male and female radiolocations were distributed in broadleaf deciduous forest in Study Area 2 than in Study Area 1. Also, female bobcats were more often located in mixed and coniferous forest and males spent more time in transitional habitats in the validation sites than in the initial study area. Seventy-eight percent of female locations occurred in areas predicted to be suitable habitat by logistic regression models (conditional randomization), whereas, 71% of male locations were classified successfully.

### Statewide Model Application

Application of logistic regression models (conditional randomization) on a cell-by-cell basis resulted in classification of 56,875 $km^2$ (48.5%) of Pennsylvania as unsuitable habitat for either male or female bobcats. An area of 18,564 $km^2$ (15.8%) was classified as suitable for both male and female bobcats, whereas 39,067 $km^2$ (33.3%) was suitable for males but not for females. As we observed in Study Area 1, regardless of modeling approach, female habitat was a subset of a broader spectrum of male habitat; only 2,791 $km^2$ (2.4%) of exclusive female habitat was identified by logistic regression models. Most suitable habitat was distributed throughout northcentral, northeast, and southcentral Pennsylvania (Fig. 3).

We used percent composition of suitable habitat ($P \geq 0.60$) as a measure to evaluate the potential of simulated ranges to support female bobcats. We selected a critical value of 25% home range composition in suitable habitat as a cut-off value in evaluating home range potential. These criteria were based on relationships between home range size and habitat composition observed on Study Area 1. We estimated the percent composition of suitable habitat within 18,770 simulated female home ranges throughout Pennsylvania. Statewide, 4,222 (22.5%) of simulated home ranges contained >25% suitable habitat.

### Statewide Model Validation

We received 128 responses from the WCOs surveyed. Twenty-one (minus non-respondents) reported bobcats were not present in their district. Forty-three percent ($n = 47$) of respondents reported that they occasionally sighted bobcats in their district, but that established populations were not present (Fig. 4). Fifty-six percent ($n = 60$) of respondents reported having established bobcat populations in their districts. Average percent composition of male and female habitat was higher in districts reporting established populations ($\bar{x} = 38.2\%$ and 20.5% for M and F habitat, respectively) than in those reporting occasional sightings ($\bar{x} = 30.0\%$ and 16.0% for M and F habitat, respectively). Similarly, average percent of simulated home ranges within each district that contained suitable amounts of habitat was greater in districts reporting established populations ($\bar{x} = 31.1$) than in those reporting occasional sightings ($\bar{x} = 14.7$; $t = -4.93$, $P \leq 0.001$).

The percent area of each district believed to support bobcat populations was reported as 1–10% ($n = 7$), 11–25% ($n = 15$), 26–50% ($n = 11$), 50–75% ($n = 19$), and >75% ($n = 8$). Districts described as containing >75% suitable habitat were located in northcentral and northeastern Pennsylvania. We compared the percent composition of male and female habitat within WCO districts to serve as a subjective, statewide validation of the modeling effort. The categorical estimate of percent of each district supporting bobcats was positively correlated to the percent composition of male ($r = 0.68$, $P < 0.001$) and female ($r = 0.52$, $P < 0.001$) habitat as estimated by statewide application of logistic habitat models. Estimates of percent habitat in WCO districts were generally lower than the percent area predicted as suitable by the logistic regression models. Percent of each district supporting bobcats was also positively correlated to the percent of simulated female home ranges which contained >25% suitable habitat ($r = 0.46$, $P < 0.001$).

Six-hundred thirty-nine bobcat mortalities (92% from roadkills) were recorded from 1986–99 in 44 of 67 Pennsylvania counties (Fig. 5). The majority of mortalities were reported in counties throughout the northcentral, northeastern, and southcentral regions, which matched the habitat model well (Fig. 3). Mortalities were also occasionally reported in several southeast and southwest counties.

## DISCUSSION

### Bobcat Home Range Size and Habitat Selection

Bobcats in northcentral Pennsylvania exhibited strong slope and aspect associations. We suspect these associations related to differences in understory structure and prey availability, as reported by Litvaitis et al. (1986) in Maine. Male and female bobcats in northcentral Pennsylvania selected broadleaf deciduous forest during summer and winter. Females avoided herbaceous and unvegetated areas during summer and winter. However, males avoided herbaceous areas during summer and mixed forest, unvegetated areas, and perennial herbaceous types during winter.

Home range size of male bobcats in Pennsylvania averaged 82 $km^2$ (median = 42 $km^2$). This estimate was highly variable, but was comparable to estimates from other northeastern states. Fox (1982) reported average male home ranges of 36–326 $km^2$ in New York State, and estimates of male bobcat home range size in Maine ranged from 71–112 $km^2$ (Litvaitis et al. 1986). Similarly, estimates of female home range size in Pennsylvania were comparable to estimates of 28–33 $km^2$ in Maine (Major 1983).

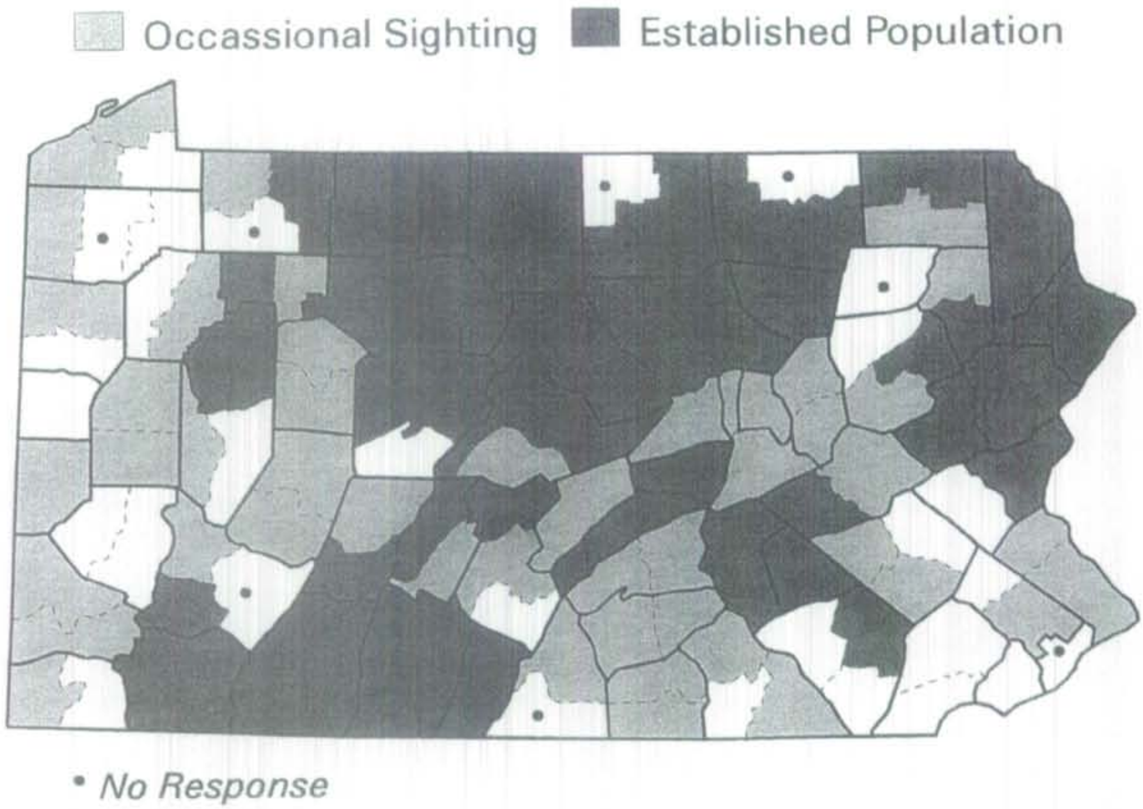


Fig. 4. Distribution of established bobcat populations and of occasional sightings throughout Pennsylvania as reported by Wildlife Conservation Officers during 1994.

Other studies of bobcat behavior have demonstrated intersexual differences in activity, prey use, and habitat selection (Heller and Fendley 1982, Litvaitis et al. 1984, Rolley and Warde 1985, Litvaitis et al. 1986, Lovallo and Anderson 1995). Intersexual differences in habitat selection and home range size that we observed were likely attributed to sex-related size dimorphism exhibited by bobcats throughout the northeast (Gittleman 1989). Although we detected seasonal effects on habitat selection, we chose not to develop season-specific habitat models because we were interested in developing models that predicted habitat suitability on an annual basis and because sample size was limited during summer periods. Significant intersexual differences in cover type use and the association of physiographic characteristics warranted the development and application of sex-specific habitat models.

**Mahalanobis Distance Models**

Models based on direct spectral band intensity, slope, and aspect produced a map depicting various levels of habitat suitability scaled from 0.0 (unsuitable) to 1.0 (suitable). Although suitability scores were based on *P*-values, these values were only interpreted as a relative scaling, rather than a probability that bobcats would be present, survive, or reproduce in a particular geographic cell (Knick and Dyer 1997). By directly modeling from spectral reflectance, we made no *a priori* assumptions of habitat or cover type suitability and thereby avoided errors inherent to classification of remotely sensed data. Reflectance data provided spatial information on occurrence and gradients of a variety of vegetative conditions (e.g., stand structure, density of understory vegetation, soil moisture) that may potentially influence habitat selection, but are difficult to represent in a traditional cover-type or habitat mapping approach. Others have detected significant relationships among various forest structure elements and direct spectral band intensity such as the leaf area index, tree density, diameter at breast height, and tree age (Peterson et al. 1986, Running et al. 1986).

Mahalanobis distance-based models successfully predicted the spatial occurrence of bobcats in Study Area 1 and in independent validation sites. Cover type composition and physiographic characteristics associated with areas predicted as suitable habitat by Mahalanobis distance-based models were consistent with patterns of habitat selection estimated from univariate analyses. These results support the use of Mahalanobis distance and direct spectral reflectance as a method to extrapolate multivariate patterns of habitat selection within the geographic extent of model construction.

**Logistic Regression Models**

Parameter estimates for multiple logistic regression models developed using random points were similar to

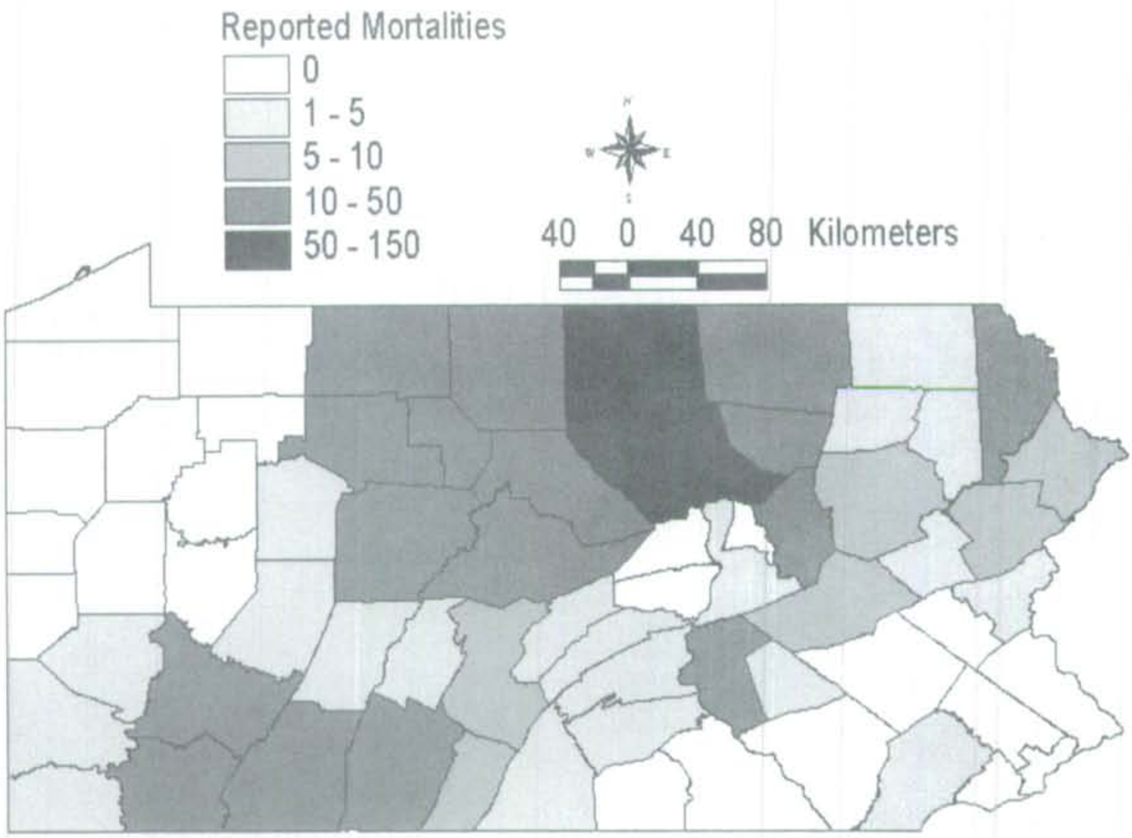


Fig. 5. Spatial distibution of bobcat mortalities ($n$ = 369) reported by Pennsylvania counties during 1986–99.

those estimated using the conditional random approach. For example, models from both approaches included negative parameter estimates for herbaceous and unvegetated areas for males and females. Broadleaf deciduous forest had a strong positive influence on male bobcat presence for both approaches as did broadleaf deciduous forest and mixed forest for females. A notable difference was that multiple logistic regression models developed from conditional randomization for females included conifer forest and did not include slope as a significant effect. By using only random points that occurred in areas predicted as unsuitable by the Mahalanobis models, we improved overall classification success of the model by 6% for males and 3% for females.

We observed an inverse correlation between home range size and percent composition of areas classified as suitable habitat; this relationship was particularly strong for females. This relationship became increasingly significant as suitability scores increased suggesting that associated $P$- values reflected gradients in habitat suitability that were linked to the ability of individuals to acquire resources within home ranges.

**Selecting an Approach for Statewide Model Extrapolation**

The ability of Mahalanobis distance-based models and logistic regression models to predict the spatial occurrence of female bobcats was greater within the validation site than that estimated by cross-validation within the geographic extent of model construction. The ability of Mahalanobis distance-based models to predict the spatial occurrence of male bobcats was greater in Study Area 1and decreased by 13% when applied to Study Area 2. Predictive success of logistic regression models for males was 7% greater in Study Area 2 than that estimated by cross-validation in Study Area 1. It is unknown whether these differences were due to differences in cover type availability between areas, individual variation in habitat selection, or within-scene variance of spectral reflectance in the case of Mahalanobis distance models. No study area boundaries were delineated in the validation site that could be used to determine cover type availability because bobcats were dispersed across an extensive area.

Within Study Area 1, classification rates for Mahalanobis distance-based models were greater than those of logistic regression models by $\leq$18% for females and 21% for males. Similarly, spectral-based models successfully predicted the spatial occurrence of bobcats in the validation site at a greater rate than did logistic regression models. Although spectral-based models had greater predictive success, anticipated spectral variance among Thematic Mapper scenes and differences in scene dates precluded extrapolation of models based on spectral reflectance to other regions of Pennsylvania. The use of conditional randomization in the logistic regression models provided a method to incorporate the predictive success of Mahalanobis models into a statewide effort to model the extent and distribution of suitable bobcat habitat.

Model predictions of the statewide distribution of potential female home ranges was geographically consistent with previous reports of established bobcat populations in Pennsylvania (Giles 1986, Merritt 1987). This result suggested that amount and pattern of suitable female habitat, as predicted by multivariate models of habitat selection, may directly relate to potential statewide bobcat distribution. Our method to delineate potential female home ranges was based on percent habitat composition of the home range (e.g., >25%). These results are conservative because female bobcats likely occupy larger home ranges with smaller proportions of suitable habitat beyond the geographic extent identified in these analyses.

**Statewide Model Validation**

Our results indicated a positive statewide validation of habitat models. Wildlife Conservation Officers consistently overestimated the area capable of supporting bobcats in their districts as predicted by habitat selection models. This result was not surprising because habitat models were developed to identify selected habitat components and these components only comprised a portion (e.g., 18–45%) of a bobcats home range. It is likely that WCOs considered all areas a bobcat might be encountered (e.g., home range) while subjectively estimating the proportion of their district capable of supporting bobcats. We observed general spatial correspondence between the statewide distribution of suitable female home ranges and WCO reports of established populations, sightings, and incidental captures by trappers. Similarly, statewide data on the location of reported bobcat mortalities provided general correspondence with the WCO survey results and statewide habitat modeling results.

## CONCLUSIONS

The statewide application of multivariate habitat selection models for bobcats in Pennsylvania provides an information source for habitat-based management decisions and serves as a basis to develop hypotheses concerning local- and landscape-level habitat associations. Further regional validation should be conducted to better understand geographic variability in bobcat-habitat relationships and to improve predictive success of habitat suitability models.

## ACKNOWLEDGMENTS

This research was a cooperative effort among the School of Forest Resources, The Pennsylvania Cooperative Fish and Wildlife Research Unit, and the PGC. Jack Giles, former PGC wildlife biologist, coordinated bobcat tagging efforts and radiotelemetry monitoring. We thank George Baumer for providing access to GIS facilities at The Office of Remote Sensing of Earth Resources.

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# IMPACTS OF REESTABLISHED FISHERS ON BOBCAT POPULATIONS IN WISCONSIN

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***Abstract***: Bobcats (*Lynx rufus*) and fishers (*Martes pennanti*) are allopatric over much of their geographic ranges, but converge in the upper Great Lakes region. We examined evidence for consumptive, territorial, and encounter competition between bobcats and fishers in northern Wisconsin during 1991–95. Such evidence included use of shared resources, spatial interaction, and impacts on 7 bobcat population parameters. Bobcats did not change their diets in the presence of fishers, but fisher diets contained a greater proportion of small mammalian prey and less deer when bobcats were relatively common, suggesting bobcat interference with deer consumption by fishers. Bobcats and fishers did not avoid each other as indicated by overlapping home ranges and by simultaneous paired locations of individual bobcats and fishers when home ranges did overlap. Thus, there was no evidence of territorial competition between these species. Impacts of interference competition were not detected in measured demographic parameters. Encounter competition or predation was inferred from the increase in bobcat kitten mortality and reduction in bobcat population growth. Competition between bobcats and fishers was weak and should result in equilibrium as predicted.

***Key words***: bobcat, competition, fisher, interspecific interactions, *Lynx rufus*, *Martes pennanti*, sympatric carnivores, Wisconsin.

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Bobcats (*Lynx rufus*) and fishers (*Martes pennanti*) are now, and historically have been, allopatric over much of their geographic ranges. Bobcats reach their northern limit in southern Canada (McCord and Cardoza 1982), whereas fishers rarely extend into the U.S. (Strickland et al. 1982). Sympatry occurs in New England, the northern Rockies, and the Great Lakes states. Wisconsin is one of the few areas in North America where bobcats and fishers coexist and offers a unique opportunity to study their interrelationships.

Bobcats were present in Wisconsin prior to European settlement. Habitat changes that took place in the early part of the 20th century benefitted bobcats; older forests were cut and younger forests, with their associated fauna (e.g., snowshoe hares [*Lepus americanus*] and white-tailed deer [*Odocoileus virginianus*]), provided increased food. Bobcats are currently resident in northern Wisconsin and the population supports annual harvests of up to 250 animals (Dhuey 1995).

Fishers were also present in all forested regions of Wisconsin prior to European settlement (Jackson 1961, Pils 1983). Fishers were extirpated in the 1920s due to over-harvest and habitat alteration, which concurrently benefitted bobcats (Powell 1982, Pils 1983). In the 1950s and 1960s fishers were reintroduced to the Nicolet and Chequamegon National Forests (Pils 1983), and protected refuges were established around release sites. Fishers did well following release (Kohn and Creed 1983), and their populations continued to grow and increase in distribution. Wisconsin fisher populations now sustain annual harvests of approximately 1,500 animals (Dhuey 1995).

The evaluation of the fisher restoration effort on Wisconsin's bobcat populations is of interest from a conservation perspective. Success of a restoration effort can be questioned if the reintroduced species has a negative effect on a resident species, especially if that resident species is already rare or at low densities. Bobcats and fishers occur at relatively low densities (0.1 individuals/km$^2$ for bobcats and 0.5 individuals/km$^2$ for fishers) and are at the edge of their continental range in Wisconsin. Species at range margins are likely to experience different influences of natural selection than those at the center of their range (Lesica and Allendorf 1995) due to exposure to conditions not experienced by species near range cores. These influences may assist us in understanding the role that competition plays in determining species' range limits. The interaction of fishers and bobcats in northern Wisconsin potentially represented one such case.

There was some indirect evidence that fishers were adversely impacting Wisconsin bobcat populations as early as 1975. The average annual harvest of bobcats from northern Wisconsin declined from 43 bobcats/county in 1963 to 13 bobcats/county in 1976 (Creed and Ashbrenner 1976). Klepinger et al. (1979) attributed these early declines in harvest to a reduction in the bobcat population and not to declines in other factors which may influence harvests (e.g., reduced trapper effort). The average bobcat harvest per county declined further to 10.8 in 1991 (Dhuey 1992). Further, the ratios of kittens to adult females and juveniles to adult females in the bobcat harvest sample were lower in counties with fishers classified as common than in counties with fishers classified as uncommon (W.A. Creed, Wisconsin Department of Natural Resources, personal communication). No differences were detected in average litter sizes between bobcats harvested from these 2 groups of counties, and Creed suggested that the observed differences in ratios were due to fisher predation on the bobcat kitten and juvenile age classes. Our objectives were to (1) document food habits for bobcats and fishers to determine the extent of shared use of food resources, (2) determine whether sympatric bobcats and fisher home ranges overlap, and (3) examine 7 bobcat demographic parameters in relation to fisher abundance for evidence of competition.

## STUDY AREA

The study took place in the northern forest region of Wisconsin (Curtis 1959) (Fig. 1). Animals were captured and radiocollared on 3 primary study areas: the Chequamegon National Forest (CNF), Nicolet National Forest (NNF), and St. Croix National Riverway (SCNR). There is little topographic relief in northern Wisconsin with a maximum elevational change of only 400 m. The region is underlaid with pre-Cambrian bedrock over which glacial drift has been deposited. The soils are largely podzols, but vary from thin rocky soils to deep loams and clays (Curtis 1959). The climate is variable with cold, snowy winters. Mean January temperature is -11°C and mean July temperature is 18°C. Average annual precipitation is 74 cm of water-equivalents. Average snowfall is 125 cm.

Curtis (1959) described the northern forests as containing a wide variety of vegetational types. The forests are typically characterized by the presence of conifers, but a large hardwood component is also present. The lowland forests contain either conifer swamps with black spruce (*Picea mariana*), tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*) as the most common species; or hardwood swamps dominated by black ash (*Fraxinus nigra*) or yellow birch (*Betula lutea*). The uplands support jack pine (*Pinus banksiana*) or red pine (*P. resinosa*) on the lighter sandy soils, or white pine (*P. strobus*) on the sandy loams. Conifer-hardwood mixed forests with white pine, eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saacharium*), basswood (*Tilia americana*) and yellow birch occupy the richer soils.

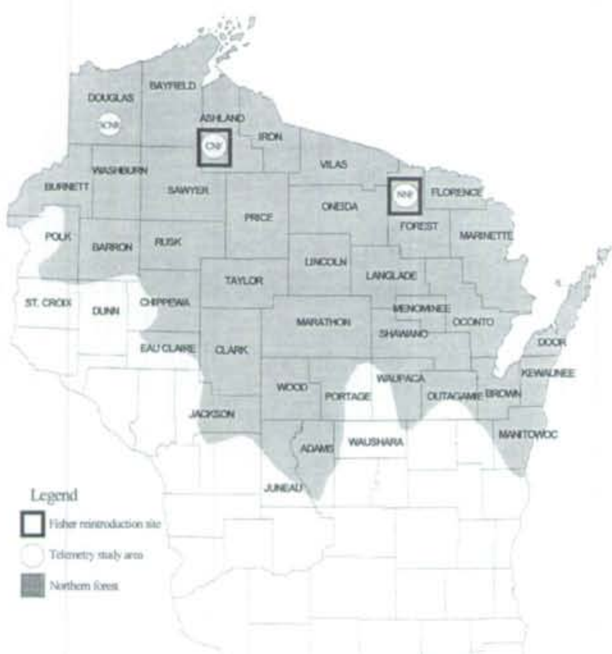


Fig. 1. Location of the northern forest region of Wisconsin (after Curtis 1959). Fisher reintroduction sites and radiotelemetry study areas are delineated (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway).

## METHODS

Connell (1983) described field experiments to measure interspecific competition in which the abundance of one species is changed and the response of the other species is documented. The response measured is usually (1) a change in density, (2) a change in a parameter which could affect density (e.g., fecundity, survival, body fat content), or (3) a change in resource used or in occupied habitat. Under hypotheses of consumptive, encounter (i.e., predation), and territorial competition, we made a number of predictions (Table 1) about the relationship of fisher density to 7 bobcat population parameters. Each hypothesis of competition had an associated series of assumptions and predictions related to the parameters. We evaluated the pattern of responses of bobcat population demography to fisher abundance based on the predictions (Table 1) and used these results to infer competition and to distinguish among the types of competition when possible. For example, consumptive and territorial competition were distinguished by the segregation of home ranges or the avoidance between individuals within home ranges.

We partitioned study areas according to the relative abundance of fishers. Because fisher and bobcat carcasses obtained from hunters and trappers were the source of most population parameters, and the location of kill was recorded only by county, the county was the geographic area for assessing relative fisher abundance. Counties were classified as having either relatively common (C) or relatively scarce (S) fisher populations.

### Relative Abundance

We used track counts in snow on 37 16-km transects (Wisconsin Department of Natural Resources, unpublished data) to estimate relative abundance of predator and prey species. Each transect was coded for the presence or absence of bobcats, fishers, and hares, and regression analysis was used to determine the probability of encountering bobcat tracks with fisher and/or hare tracks. Temporal differences in bobcat, fisher, and hare track observation rates during 1991–95 were explored using ANOVA. The relationship among the number of fisher tracks observed per transect, the distance the transect was from the nearest fisher release site, and the year of census was estimated using multiple linear regression.

Table 1. Predictions of 7 population parameters which result from hypotheses of consumptive, territorial, or encounter competition.

| Parameter | Consumptive competition | Territorial competition | Encounter competition |
|---|---|---|---|
| Kitten survival | Survival rates of bobcat kittens are lower where fishers are common than where scarce | Survival rates of kittens are lower where fishers are common than where scarce | Survival rates of kittens are lower where fishers are common than where scarce |
| Adult survival | Survival rates of adult bobcats are lower where fishers are common than where scarce | Survival rates of adults are lower where fishers are common than where scarce | Survival rates of adults are unrelated to fisher density |
| Fecundity | Bobcat reproductive rates are lower where fishers are common than where scarce | Bobcat reproductive rates are lower where fishers are common than where scarce | Bobcat reproductive rates are unrelated to fisher density |
| Body condition | Bobcat condition indices are lower where fishers are common than where scarce | Bobcat condition indices are lower where fishers are common than where scarce | Bobcat condition indices are unrelated to fisher density |
| Population growth | As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density | As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density | As a consequence of reduced kitten survival, bobcat population growth will be inversely related to fisher density |
| Population density | As a consequence of of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density | As a consequence of reduced survival and fecundity, bobcat population growth will be inversely related to fisher density | As a consequence of reduced kitten survival, bobcat population growth will be inversely related to fisher density |
| Home range | Bobcat home ranges will be larger where fishers are common than where scarce | Home ranges of fishers and bobcats will be spatially separate or will avoid each other while within home ranges | Bobcat home ranges will be unrelated to fisher density |

Relative abundance maps for bobcats and fishers were generated in ArcInfo (ESRI, Redlands, California, USA) using information from track counts and location-specific harvests. A discrete distribution of the numbers of tracks observed/transect was interpolated to a continuous distribution of tracks across the northern-forest study area using an inverse distance weighting function in ArcView Spatial Analyst (ESRI, Redlands, California, USA). A continuous distribution of harvests was created using a focal-mean smoothing technique on location-specific harvests. The relationship between county-level track counts and harvests was explored by correlation analysis. Track-count and harvest-distribution maps were merged to produce maps of relative abundance for fishers and bobcats. Weighted averages of relative abundance values were calculated for each of the 18 counties, and counties were classified as either above the mean abundance value (common) or below the mean abundance value (scarce).

Relative abundance of snowshoe hares was determined as was done for bobcats and fishers except that only track counts were used. Location-specific information on hare harvest was unavailable. Estimates of deer density were obtained for each deer management unit in the study area (Vander Zouen and Warnke 1995). Relative abundance maps were created for deer using unit-specific density information.

Relationships among the relative density of fishers, bobcats, hares, and deer were examined. One thousand random points were placed on the maps of relative abundance. Of these, 740 were within the northern-forest study area and intersected the bobcat, fisher, hare, and deer maps. Relative abundance values were appended to each point for each species. Multiple linear regression ($P = 0.1$ to enter forward selection procedures) was then used to examine the relationships among bobcat, fisher, hare, and deer relative densities.

Track counts and trapping were used as indices of abundance on the 3 smaller study areas. Track counts were conducted at least twice monthly following the methodology described above except for snowshoe hares. Hare tracks were noted as present or absent in every 160-m block along each 16-km transect for a total of 100 blocks/transect. Track counts on each study area were summarized as the number of bobcat and fisher tracks observed/transect, and the percentage of 160-m blocks with hare tracks. Live-trapping rates (animals captured/ 1,000 trap-nights) were used to assign relative abundance values for bobcats and fishers, and track counts were used to classify hare abundance for each study area.

**Animal Capture and Radiotelemetry**

Bobcats were captured with Number 3 Victor "soft-catch" foot-hold traps (Woodstream Co., Lititz, Pennsylvania, USA) and fishers were captured using Tomahawk box traps (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) with a single door opening 22 cm on a side. Bobcats and fishers were immobilized with ketamine HCl and xylazine (10:1 mixing ratio) at a dose of 10 mg/kg body weight. Animals were aged as kitten, juvenile, or adult based on size, cranial development (Strickland et al. 1982), and tooth eruption (Crowe 1975). All were weighed, measured, inspected for injuries or parasites, and uniquely tattooed inside an ear. Those individuals judged to be adults were radiocollared (Advanced Telemetry Systems, Isanti, Minnesota, USA).

Radiocollared bobcats and fishers were located $\leq 8$ times weekly during winter (Nov–Mar), and less frequently during the rest of the year. Locations were estimated from 2–3 bearings using a computer program. Bearing error determined from 10 transmitters placed at known locations averaged $5.5^{\circ}$ (SE = 0.1).

**Home Range Analysis**

Because competition for space and food should be most manifest when resources are in short supply, winter locations were used in home range analyses, and then only when separated by $\geq 6$ hr to minimize autocorrelation of locations (Swihart and Slade 1985). Home ranges were delineated using the minimum-area method (MCP) (Hayne 1949) from animals with >30 locations during a single winter. We used *t*-tests ($\alpha = 0.05$) to test for differences in the sizes of home ranges between sexes, species, and study areas.

Area of home-range overlap was calculated for intersecting home-range pairs. For species pairs (bobcat-fisher) with intersecting home ranges, avoidance behavior was inferred from the distribution of distances between telemetry locations taken within 2 hr of each other as compared to distances between random points within the 2 home ranges. We constructed a frequency distribution of separation distances between bobcats and fishers. This observed distribution was compared with the distribution of random distances expected if the animals behaved independently using Chi-square.

**Carcass Examination**

Hunters and trappers were required to surrender carcasses of harvested fishers and bobcats. The carcasses were collected by WDNR for age determination and for counts of corpora lutea or placental scars. Subsequently, the carcasses were transported to the Great Lakes Indian Fish and Wildlife Commission laboratory to extract fat bodies and examine stomach contents.

*Age and Fecundity.*—Bobcat ages were determined from cementum annuli (Crowe 1972, Kelly 1977) and used to obtain age-specific fecundity rates, carcass conditions, and food habits. Individuals >1 year were classified as kits, between 1–2 years as yearlings, and older animals as adults.

Litter size was estimated from counts of placental scars (Wright and Coulter 1967, Crowe 1975). Differences in bobcat pregnancy rates between areas where fishers were common vs. scarce were assessed using t-tests. Analysis of variance was used to examine differences in bobcat litter size due to age, year, and relative fisher abundance.

*Condition Index.*—An index to carcass condition was developed which used a kidney fat index (KFI) (Kirkpatrick 1980) in a non-linear model to predict lipid content of skinned carcasses (J. H. Gilbert, unpublished data). Once parameters were estimated in the model, it was run using the KFI inputs from the sample of bobcat carcasses. Analysis of variance was used on the resulting estimates of the proportion of body mass consisting of lipids to examine differences due to species, age, sex, year, and fisher abundance.

*Food Habits.*—Stomach contents from harvested bobcats and fishers were separated by food item and weighed. We calculated frequency of occurrence of each food item (i.e., the proportion of all stomachs containing that food item) and proportion biomass (i.e., the proportion of stomach biomass consisting of a particular food item). Chi-square analysis was used to detect differences in the frequency of occurrence of food items in stomach contents by species, sex, and fisher abundance. Multivariate analysis of variance was used with the mean proportion of biomass of 6 food items (deer, hare, medium mammals, small mammals, birds, and vegetation) as response variables to examine effects due to species, age, sex, year, and fisher abundance on biomass measures. Food diversity (Shannon and Weaver 1949) was calculated for each species and sex.

**Population Growth**

Trends in annual snow-track counts during 1991–95 were used to index population growth of bobcats. The instantaneous rate of population increase was estimated both for the study area as a whole and for C and S counties separately from the slope of the line relating the natural log of the mean number of tracks observed on snow-track transects and the year of observation. An alpha of 0.1 was used for all statistical tests involving track counts.

**Survival**

Adult survival rates of bobcats were estimated from radiotelemetry and life table analysis. Winter survival estimates were obtained from MICROMORT (Heisey and Fuller 1985). Only winter survival estimates were derived because animals were only monitored intensively in winter and all observed bobcat deaths occurred during this season. Life tables were constructed from the sample of bobcats harvested during 1991–95, and age-specific survival rates for adult bobcats were calculated using the resulting age distributions.

**Population Modeling**

Kitten and yearling survival rates were derived from population modeling. Two deterministic population models in the form of a Leslie Matrix (Leslie 1945, 1948) were constructed; one each for counties where fishers were common or scarce. Model inputs required were age-specific fecundity and survival rates. Fecundity rates obtained from carcass examination and adult survival from telemetry and life tables were kept constant in each model run. Yearling survival was set halfway between adult survival and kitten survival. Kitten and yearling survival rates were adjusted in successive runs so that the final model output provided a rate of population increase similar to that calculated from location-specific winter track counts. Adult bobcats were modeled to age 15, the age of the oldest individual harvested.

## RESULTS

**Relative Abundance**

Populations of bobcats, fishers, and snowshoe hares, as indexed by track counts and harvests, were not uniformly distributed across northern Wisconsin. Bobcat relative abundance was positively related to hare and deer abundance ($F_{2,35}$ = 120.90, $P < 0.001$), but was unrelated to fisher abundance ($F_{1,35}$ = 0.19, $P$ = 0.660).

Average number of tracks observed were 0.26 (SE = 0.04) and 4.5 (SE = 0.3) for bobcats and fishers, respectively, during 1991–95. An average of 14.7% (SE = 0.48) of transect sub-blocks had hare tracks present. The frequency of fisher tracks observed/transect ranged from 2.6 in 1991 to 6.4 in 1995 and increased over years ($F_{1,4}$ = 3.82, $P$ = 0.040). Bobcat tracks ranged from 0.17/transect in 1992 to 0.33 in 1994, but did not differ over years ($F_{4,4}$ = 0.59, $P$ = 0.672). There was significant annual variation in the percent of transect sub-blocks with hare tracks ($F_{1,4}$ =2.39, $P$ = 0.010). There was a positive relationship between presence of bobcat tracks vs. fisher ($X^2_2$ = 6.20, $P$ = 0.020) and hare ($X^2_2$ = 18.80, $P < 0.001$) tracks.

The number of fisher tracks observed/transect was positively related to year ($F_{1,4}$ = 6.12, $P$ = 0.010) and distance from nearest reintroduction site ($F_{1,35}$ = 27.16, $P < 0.001$). Fisher tracks appeared at later years on transects which were further from reintroduction sites than on transects closer to reintroduction sites.

An average of 146 bobcats and 1,367 fishers were harvested annually in Wisconsin over the study period. Harvested bobcats ranged from 71 in 1991 to 217 in 1992 and harvested fishers ranged from 204 in 1991 to 2,081 in 1994. The index of relative abundance was determined from harvest rates (harvest/100 km$^2$) and track observation rates (tracks/transect). These independent measures of relative abundance were correlated (bobcats: $r$ = 0.62; fishers: $r$ = 0.51), thus supporting their combined use to index relative abundance. The index of relative abundance of bobcats calculated from tracks and harvests ranged from 0.34 in Bayfield County to 1.56 in Florence County, and averaged 0.77 (Table 2). Eight of the 18 counties had an index >0.77, and bobcats were thus classified as being common (C). In the remaining 10 counties, bobcats were classified as scarce (S). The index of relative abundance of fishers ranged from 2.83 in Burnett County to 9.87 in Sawyer County (Table 2). Ten counties had an index >7.22, and fishers were classified as common (C). In the remaining 8 counties, fishers were classified as scarce (S).

We classified CNF and SCNR as having relatively more bobcats than NNF because these study areas had higher bobcat capture rates ($t_3$ = 2.62, $P$ = 0.040) than did NNF (Table 3). There were more bobcat track encounters on CNF and SCNR than NNF, which supported this classification, but this difference was not significant ($t_3$ = 0.94, $P$ = 0.368). Similarly, we classified the CNF and NNF as having relatively more fishers than SCNR because of higher capture rates ($t_3$ = 3.54, $P$ = 0.030) (Table 3). There were more fisher track encounters on CNF and NNF than SCNR supporting the classification, but again this difference was not significant ($t_3$ = 1.67, $P$ = 0.12). We classified CNF and SCNR as having relatively more snowshoe hares than NNF because the CNF and SCNR had significantly higher number of tracks present than did NNF ($t_3$ = 2.48, $P$ = 0.026) (Table 3).

**Home Range Analysis**

Sixteen bobcats (10 M, 6 F) and 44 fishers (27 M, 17 F) were caught on the CNF study area during 1992–95. Of the 16 radiocollared bobcats and 20 radiocollared fishers, 9 bobcats (5 M, 4 F) and 13 fishers (7 M and 6 F) lived for ≥1 winter and each yielded 30–61 locations. Mean home range size of bobcats was 69 km$^2$ for males and 28 km$^2$ for females (Table 4). Mean home range size of fishers was 20 km$^2$ for males and 7 km$^2$ for females (Table 5).

Twenty-two fishers (10 M, 12 F) and 4 bobcats (1 M, 3 F) were captured on the NNF study area during 1992–95 (Wright 1999). Eight fishers (3 M, 5 F) and 3 bobcats (1 M, 2 F) lived for ≥1 winter and each provided 31–91 locations. The male bobcats had a home range size of 58 km$^2$ and the female bobcats had a mean home range size of 19 km$^2$ (Table 4). Mean home range sizes of fishers were 10 km$^2$ for males and 6 km$^2$ for females (Table 5).

Nineteen bobcats (11 M, 8 F) and 1 fisher (M) were captured on the SCNR study area during 1991–93 (Lovallo 1993). Seven bobcats (4 M, 3 F) and the fisher survived ≥1 winter and each yielded 31–110 locations. Mean home range size of male bobcats was 41 km$^2$ and that of females was 31 km$^2$ (Table 4). The fisher home range was 13 km$^2$ in size.

Eight of the possible 16 bobcat home range pairs intersected on CNF. All of the intersecting home-range pairs included ≥1 male. The mean area of home range overlap was 14 km$^2$ or 29% of mean bobcat home range size (26% for M, 46% for F). Only 4 of the 42 possible fisher home ranges intersected on CNF; the mean area of overlap was 1.1 km$^2$ or 8% of the average fisher home range size (6% for M, 17% for F). Twenty-four of the

Table 2. Comparison of bobcat, fisher, and snowshoe hare relative abundance as determined by harvest (harvest/100 km²) and track counts (tracks/transect) in counties of northern Wisconsin during 1991–95. Harvests and track counts were added to derive an abundance index (harvests + tracks). Counties above mean abundance values were rated as having common populations (C). Counties below mean abundance values were rated as having scarce populations (S).

| County | Bobcat harvest/ 100 km² | Track counts | Harvest & tracks | Bobcat abundance code | Fisher harvest/ 100 km² | Track counts | Harvest & tracks | Fisher abundance code | Hare tracks | Hare abundance code |
|---|---|---|---|---|---|---|---|---|---|---|
| Ashland | 0.26 | 0.15 | 0.41 | S | 3.39 | 3.80 | 7.19 | S | 15.09 | C |
| Bayfield | 0.18 | 0.16 | 0.34 | S | 3.44 | 3.72 | 7.15 | S | 14.93 | C |
| Burnett | 0.71 | 0.71 | 1.42 | C | 1.28 | 1.55 | 2.83 | S | 13.17 | S |
| Douglas | 0.44 | 0.45 | 0.90 | C | 2.03 | 3.59 | 5.62 | S | 13.96 | S |
| Florence | 0.80 | 0.77 | 1.56 | C | 4.30 | 3.77 | 8.07 | C | 13.76 | S |
| Forest | 0.56 | 0.41 | 0.97 | C | 4.47 | 5.35 | 9.82 | C | 14.05 | S |
| Iron | 0.26 | 0.19 | 0.45 | S | 3.25 | 4.09 | 7.24 | C | 15.72 | C |
| Langlade | 0.24 | 0.27 | 0.51 | S | 4.05 | 4.55 | 8.60 | C | 14.13 | S |
| Lincoln | 0.45 | 0.27 | 0.71 | S | 3.59 | 4.06 | 7.65 | C | 15.72 | C |
| Marinette | 0.32 | 0.30 | 0.62 | S | 1.92 | 1.40 | 3.32 | S | 13.69 | S |
| Oconto | 0.20 | 0.22 | 0.42 | S | 1.46 | 1.39 | 2.85 | S | 12.90 | S |
| Oneida | 0.40 | 0.29 | 0.69 | S | 4.27 | 4.54 | 8.80 | C | 13.87 | S |
| Price | 0.67 | 0.28 | 0.95 | C | 3.99 | 4.24 | 8.22 | C | 16.84 | C |
| Rusk | 0.45 | 0.32 | 0.77 | C | 3.40 | 6.14 | 9.53 | C | 17.31 | C |
| Sawyer | 0.39 | 0.24 | 0.63 | S | 3.83 | 6.04 | 9.87 | C | 15.48 | C |
| Taylor | 0.51 | 0.27 | 0.79 | C | 1.55 | 3.67 | 5.21 | S | 17.96 | C |
| Vilas | 0.22 | 0.30 | 0.53 | S | 3.30 | 5.15 | 8.45 | C | 13.51 | S |
| Washburn | 0.61 | 0.74 | 1.14 | C | 2.06 | 3.93 | 5.99 | S | 15.03 | C |
| Means | 0.43 | 0.35 | 0.77 | — | 3.09 | 3.94 | 7.22 | — | 14.84 | — |

Table 3. Relative abundance index measures for bobcats and fishers on 3 study areas (CNF: Chequamegon National Forest, NNF: Nicolet National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during 1991–95. An abundance rating of C indicates common populations and S indicates scarce populations.

| | Bobcat | | | Fisher | | | Snowshoe hare | |
|---|---|---|---|---|---|---|---|---|
| Study area | Captures[a] | Track counts[b] | Rating | Captures[a] | Track counts[b] | Rating | Track counts[b] | Rating |
| CNF- | 6.50 | 0.40 | C | 34 | 7.60 | C | 32 | C |
| NNF | 1.50 | 0.10 | S | 15 | 6.00 | C | 14 | S |
| SCNR | 5.80 | 0.35 | C | 2 | 1.40 | S | 34 | C |

[a]Per 1,000 trap-nights.
[b]Per 16-km transect.

Table 4. Sizes (km²) of bobcat home ranges on 3 study areas (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during winter.

| Study area | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | $n$ | $\bar{x}$ size (range) | $\bar{x}$ locations (range) | $n$ | $\bar{x}$ size (range) | $\bar{x}$ locations (range) |
| CNF | 5 | 69 (36–86) | 45 (30–55) | 4 | 28 (22–30) | 41 (30–45) |
| NNF | 1 | 58 | 46 | 2 | 19 (16–24) | 54 (33–75) |
| SCNR | 4 | 41 (20–98) | 51 (31–80) | 3 | 31 (22–38) | 77 (37–110) |

Table 5. Sizes (km²) of fisher home ranges on 3 study areas (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin during winter.

| Study area | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | $n$ | $\bar{x}$ size (range) | $\bar{x}$ locations (range) | $n$ | $\bar{x}$ size (range) | $\bar{x}$ locations (range) |
| CNF | 7 | 20 (6–42) | 42 (30–61) | 6 | 7 (3–14) | 39 (30–59) |
| NNF | 3 | 10 (9–13) | 58 (36–86) | 5 | 6 (3–9) | 65 (37–97) |
| SCNR | 1 | 13 | 38 | --- | --- | --- |

possible 63 interspecific pairs of home ranges intersected on CNF, including males and females of both species. The average area of home range overlap between the 2 species was 5.4 km² or 12% of the average bobcat home range size (9% for M, 20% for F) and 39% of the average fisher home range size (28% for M, 77% for F).

The distribution of distances between bobcats and fishers with overlapping home ranges was calculated for 24 bobcat-fisher pairs with 480 locations on CNF. The frequency distribution of separation distances for bobcats and fishers with intersecting home ranges did not differ from random ($X^2_9 = 4.21$, $P = 0.250$).

**Carcass Examination**

*Age and Fecundity*.—We aged 362 bobcats and 801 fishers harvested during 1991–95 (Table 6). Harvested bobcats ranged in age from 0.5–15.5 years. Mean adult bobcat age at harvest was 4.5 years and did not vary significantly between sexes ($t_{360} = 1.12$, $P = 0.210$). The age distribution of bobcats and fishers was skewed toward kits and yearlings.

There were 238 (134 M, 104 F) bobcats harvested in C counties and 124 (75 M, 49 F) harvested in S counties. The mean age of harvested adult bobcats did not differ between C and S counties ($F_{1,8} = 0.89$, $P = 0.370$) (Table 7). Ratios of kittens to adults and yearlings to adults in the harvest were greater for C counties than for S counties.

Forty-six percent of bobcats >0.5 year of age were pregnant (Table 8). Counts of placental scars in pregnant female bobcats >1.5 years averaged 2.4. The number of female young produced/female peaked at 5.5 years. Counts of placental scars did not differ by year ($F_{1,6} = 1.42$, $P = 0.233$).

The proportion of female bobcats ≥1.5 years that were pregnant was similar in C vs. S counties ($t_{113} = 0.61$, $P = 0.390$) (Table 9). Mean litter size in S counties (2.7 kits/litter) was greater than for C counties (2.3 kits/litter) ($F_{1,6} = 4.304$, $P = 0.044$), although the size of yearling litters was not significantly different between C and S counties ($F_{1,3} = 0.464$, $P = 0.663$).

*Condition Index*.—The proportion of bobcat biomass consisting of lipids averaged 0.13. There was no difference in the lipid content of male (0.13) and female (0.14) carcasses ($F_{5,6} = 4.06$, $P = 0.152$). There was no difference detected in bobcat lipid content between C and S counties ($F_{5,6} = 0.155$, $P = 0.694$) (Fig. 2).

*Food Habits*.—More than 85% of the total food biomass found in bobcat stomachs consisted of either deer or hare, and either one or both of these food items were found in 61% of all bobcat stomachs (Table 10). Other food items such as muskrats (*Odantra zibethica*), squirrels (*Sciurus* spp.), small rodents, and birds were present but in low amounts. Frequencies of occurrence of food items did not differ between male and female bobcats ($X^2_4 = 9.07$, $P = 0.110$), but there were differences in the mean proportional biomass ($F_{1,8} = 6.93$, $P = 0.012$). Males consumed proportionately more deer than did females ($F_{1,10} = 11.51$, $P < 0.001$), whereas females ate proportionately more hares ($F_{1,10} = 3.26$, $P = 0.039$). Female bobcats had a more diverse diet than did males as reflected by a Shannon Diversity Index of 1.05 vs. 0.75 for males (Table 10).

There were differences between male and female fishers in the frequency of occurrence of food items ($X^2_4 = 10.35$, $P = 0.070$) and in the mean proportion of food item biomass ($F_{1,10} = 11.51$, $P < 0.001$). Males consumed more hares than did females ($F_{1,10} = 7.92$, $P = 0.005$) and females ate more small mammals ($F_{1,10} = 7.82$, $P = 0.005$). Fishers had more diverse food habits than did bobcats. The Shannon Diversity Index of food habits was 1.7 and 1.6 for males and females, respectively.

There were differences between bobcat and fisher food habits as measured by frequency of occurrence ($X^2_4 = 168.80$, $P < 0.001$) (Table 10) and by the mean proportion of food biomass of each food item ($F_{1,10} = 48.55$, $P < 0.001$) (Fig. 3). Bobcats tended to consume larger prey whereas fishers ate more small and medium mammals, birds, and vegetation (fruits, nuts, seeds) than did bobcats.

Bobcat diets did not differ between C and S counties, as measured by mean proportion of food item biomass ($F_{1,10} = 0.79$, $P = 0.602$) (Fig. 4) or by frequency of occurrence ($X^2_4 = 3.78$, $P = 0.580$). Bobcats did not alter their diets based on the relative abundance of fishers. Fishers, on the other hand, consumed more smaller food items when in the presence of bobcats. Their diets varied significantly between counties with differing relative abundance of bobcats as measured by frequency of occurrence ($X^2_4 = 24.51$, $P < 0.001$) and mean proportion of food biomass in each food item ($F_{1,10} = 2.27$, $P = 0.045$) (Fig. 5). There were more deer present in fisher stomachs where bobcats were scarce than where bobcats were common ($F_{1,10} = 4.29$, $P = 0.039$), and there were more small mammals in fisher stomachs where bobcats

Table 6. Age-distribution of fishers and bobcats obtained from fur harvesters in Wisconsin during 1991–95.

| | Bobcats | | | Fishers | | |
|---|---|---|---|---|---|---|
| Age (yr) | Females | Males | Total | Females | Males | Total |
| 0.5 | 38 | 41 | 79 | 189 | 94 | 283 |
| 1.5 | 35 | 44 | 79 | 205 | 90 | 295 |
| 2.5 | 27 | 36 | 63 | 76 | 32 | 108 |
| 3.5 | 19 | 29 | 48 | 43 | 11 | 54 |
| 4.5 | 9 | 24 | 33 | 34 | 7 | 41 |
| 5.5 | 9 | 15 | 24 | 6 | 1 | 7 |
| 6.5 | 7 | 6 | 13 | 5 | 2 | 7 |
| 7.5 –15.5 | 3 | 3 | 6 | 9 | 14 | 23 |
| Totals | 147 | 198 | 345 | 567 | 251 | 822 |

Table 7. Age-distribution of bobcats harvested from counties where fishers were common or scarce in Wisconsin during 1991–95.

| | Common fishers | | | | Scarce fishers | | | |
|---|---|---|---|---|---|---|---|---|
| Age (yr) | Males | % | Females | % | Males | % | Females | % |
| 0.5 | 28 | 21 | 24 | 23 | 13 | 17 | 14 | 29 |
| 1.5 | 26 | 19 | 27 | 26 | 18 | 24 | 8 | 16 |
| 2.5 | 25 | 19 | 17 | 16 | 11 | 15 | 10 | 20 |
| >2.5 | 55 | 41 | 36 | 35 | 33 | 44 | 17 | 35 |
| Totals | 134 | — | 104 | — | 75 | — | 49 | — |

Table 8. Fecundity table for female bobcats harvested in Wisconsin during 1991–95.

| Age (yr) | Females | No. pregnant | Prop. pregnant | No. placental scars | No. female young | No. female young/ female |
|---|---|---|---|---|---|---|
| 1.5 | 48 | 12 | 0.25 | 2.5 | 15 | 0.3 |
| 2.5 | 38 | 15 | 0.40 | 2.5 | 19 | 0.5 |
| 3.5 | 28 | 16 | 0.57 | 2.8 | 23 | 0.8 |
| 4.5 | 10 | 7 | 0.70 | 2.4 | 9 | 0.9 |
| 5.5 | 7 | 5 | 0.71 | 2.6 | 7 | 1.0 |
| 6.5 | 10 | 6 | 0.60 | 2.3 | 7 | 0.7 |
| 7.5–15.5 | 10 | 9 | 0.90 | 2.1 | 10 | 1.0 |
| Total/ $\bar{x}$ | 151 | 70 | 0.46 | 2.4 | 90 | 0.7 |

Table 9. Fecundity tables for bobcats harvested from counties where fishers were classified as common or scarce in Wisconsin during 1991–95.

| Age (yr) | Females | No. pregnant | Prop. pregnant | No. placental scars | No. female young | No. female young/ female |
|---|---|---|---|---|---|---|
| Common fisher counties | | | | | | |
| 1.5 | 27 | 9 | 0.33 | 2.5 | 11 | 0.21 |
| 2.5 | 17 | 10 | 0.59 | 2.4 | 12 | 0.35 |
| >2.5 | 36 | 29 | 0.88 | 2.2 | 32 | 0.45 |
| Total/$\bar{x}$ | 80 | 48 | 0.60 | 2.3 | 55 | 0.35 |
| Scarce fisher counties | | | | | | |
| 1.5 | 8 | 3 | 0.38 | 2.0 | 3 | 0.19 |
| 2.5 | 10 | 5 | 0.50 | 2.6 | 7 | 0.33 |
| >2.5 | 17 | 14 | 0.81 | 2.7 | 19 | 0.56 |
| Total/$\bar{x}$ | 35 | 22 | 0.63 | 2.7 | 30 | 0.42 |

Table 10. Mean proportion biomass and frequency of food items found in bobcat and fisher stomachs from northern Wisconsin during 1991–95.

| | Bobcats | | | | Fishers | | | |
|---|---|---|---|---|---|---|---|---|
| | Females | | Males | | Females | | Males | |
| Food item | Frequency | $\bar{x}$ prop. biomass | Frequency | $\bar{x}$ prop. biomass | Frequency | $\bar{x}$ prop. biomass | Frequency | $\bar{x}$ prop. biomass |
| White-tailed deer | 550 | 0.46 | 85 | 0.64 | 120 | 0.16 | 98 | 0.19 |
| Snowshoe hare | 28 | 0.22 | 29 | 0.15 | 18 | 0.02 | 33 | 0.07 |
| Medium mammals[a] | 20 | 0.04 | 21 | 0.04 | 81 | 0.11 | 55 | 0.11 |
| Small mammals[b] | 17 | 0.11 | 16 | 0.06 | 147 | 0.36 | 107 | 0.28 |
| Birds | 3 | <0.01 | 6 | 0.03 | 43 | 0.05 | 40 | 0.07 |
| Vegetation | 30 | 0.17 | 18 | 0.08 | 41 | 0.30 | 165 | 0.28 |
| Total stomachs | 136 | | 173 | | 609 | | 487 | |
| Empty stomachs | 27 | | 39 | | 108 | | 91 | |
| Food-diversity index | 1.05 | | 0.75 | | 1.6 | | 1.7 | |

[a]For example, beaver, muskrat, and raccoon.
[b]For example, squirrels, voles, and shrews.

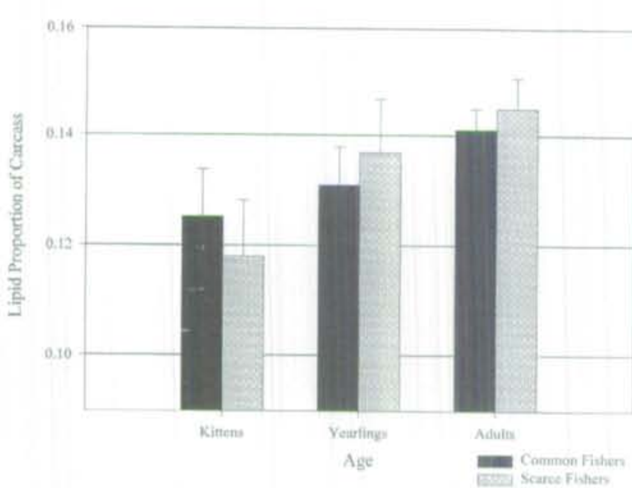


Fig. 2. Proportion of the biomass of skinned carcasses consisting of lipids in bobcats harvested in Wisconsin counties classified as having common or scarce fisher populations during 1991–95.

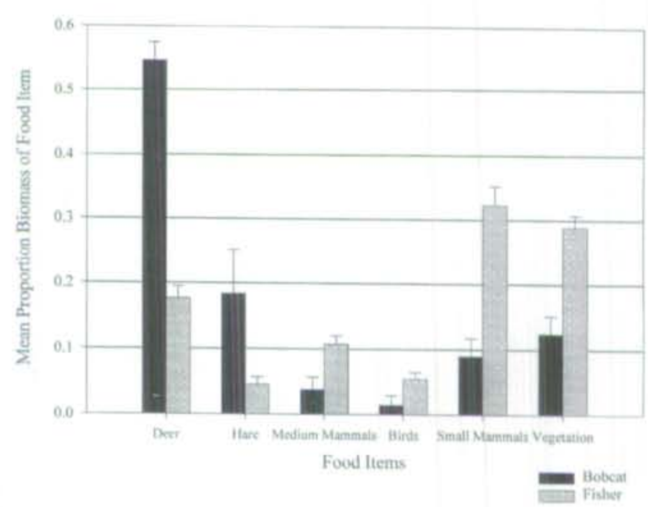


Fig. 3. Bobcat and fisher stomach contents as mean proportion of food biomass found in stomachs from animals harvested in northern Wisconsin during 1991–95.

were common as compared to where bobcats were scarce ($F_{1,10} = 3.76$, $P = 0.048$).

**Population Growth**

The mean number of bobcat tracks/transect in C and S counties ranged from 0.18–0.30 and 0.17–0.47, respectively. There was no difference in the number of bobcat tracks observed/transect in C counties ($F_{1,9} = 0.0004$, $P =$ 0.952), whereas number of tracks increased in S counties over years ($F_{1,11} = 3.007$, $P = 0.087$). The slope of the regression relating the log of number of tracks to year of observation in C counties (slope = -0.01, SE = 0.008) was not significantly different from zero ($t_4 = 0.24$, $P = 0.826$). However, the slope of the regression line for S counties (slope = 0.11, SE = 0.035) was greater than zero ($t_4 =$ 4.30, $P = 0.020$). This increase of bobcat tracks in S counties indicated an exponential rate of population increase (r) of 0.11 (SE = 0.035), or a finite rate of growth of 12% annually (Fig. 6).

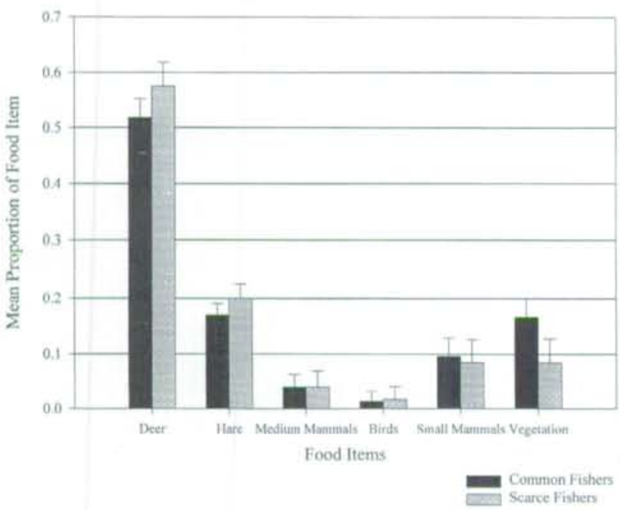


Fig. 4. Bobcat diet as mean proportion of food-item biomass found in stomachs from carcasses harvested in counties with 2 levels of bobcat abundance in northern Wisconsin during 1991–95.

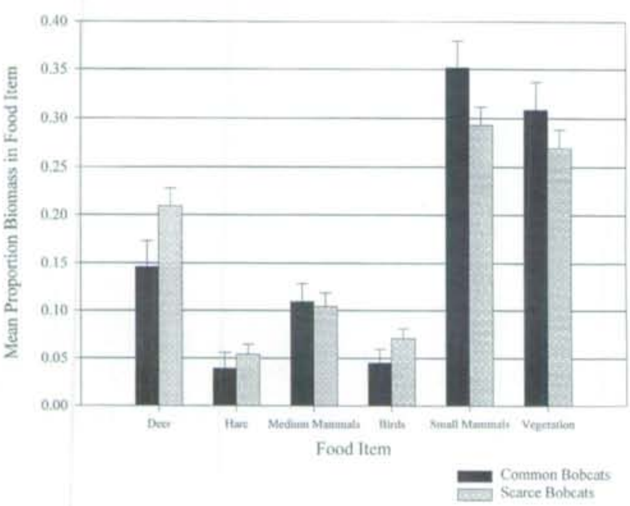


Fig. 5. Fisher diet as mean proportion of food-item biomass found in stomachs from carcasses harvested from counties with 2 levels of bobcat abundance in northern Wisconsin during 1991–95.

**Survival**

The winter survival rate of bobcats on the SCNR study area (scarce fishers) was 0.66, while winter survival on the CNF and NNF study areas (common fishers) was 0.63 and 0.57, respectively (Table 11). Likewise, survival rates of adult bobcats (>1.5) calculated from life tables did not differ between C counties (0.69) and S counties (0.67).

**Population Modeling**

A post-birth population estimate of 1,000 bobcats was established as the initial input for the model for C counties and 500 was used as the initial population size for S counties, as reflected by relative abundance. Adult survival in the population model was set to 0.62 because this was the midpoint of the range of survival estimates calculated from radiocollared bobcats and the rate reported by Fuller et al. (1995) in their review of bobcat survival studies. Kitten and yearling survival rates were arbitrarily set at 0.55 and 0.6, respectively, for the initial model run.

When the model was run for the C counties using initial inputs, the exponential rate of growth was 0.01, higher than the rate of growth estimated from track counts (-0.01). Therefore, kitten and yearling survival rates were lowered incrementally to 0.52 and 0.58, respectively. The population model with the adjusted kitten and yearling survival rates produced a population estimate which declined slightly.

When the model for S counties was run with initial inputs, the estimated exponential population growth rate was 0.01, lower than the exponential rate of growth indicated by track counts (0.11). Thus, survival rates for kittens and yearlings were incrementally raised to 0.62 for

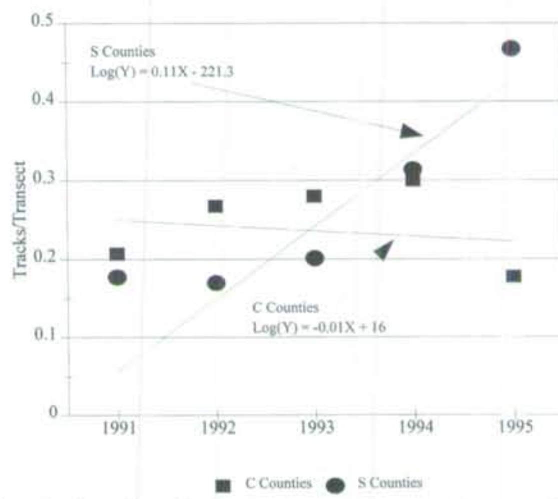


Fig. 6. Results of bobcat snow-track counts in counties with common fishers (C) and scarce fishers (S). Regression line relates $\log_{10}$ of the tracks per transect and year. The slope of this regression line is the estimated instantaneous rate of increase (r) for that bobcat population.

Table 11. Winter survival estimates for bobcats on 3 study areas (NNF: Nicolet National Forest, CNF: Chequamegon National Forest, SCNR: St. Croix National Riverway) in northern Wisconsin durng 1991–95.

| Study area | Bobcats | Radiodays | Survival | 95% CI |
|---|---|---|---|---|
| CNF | 6 | 2,880 | 0.63 | 0.36–0.99 |
| SCNR | 12 | 4,250 | 0.66 | 0.35–0.92 |
| NNF | 4 | 1,969 | 0.57 | 0.30–1.00 |

both and the resulting exponential population growth rate was 0.08. This growth rate was less than observed from track counts but no further increase of population growth was possible without kitten and yearling survival exceeding adult survival, which was highly unlikely.

## DISCUSSION

### Territorial Competition

Territorial and encounter competition both fall within the definition of interference competition (Case and Gilpin 1974). Yet some confusion exists around the everyday usage of the term interference, especially as it relates to competition for space (Schoener 1983). Interference competition has been used to describe processes as diverse as kleptoparasitism (Norris and Johnson 1998, Triplet et al. 1999), territoriality (Carbyn 1982), and predation (Paine 1966, White and Garrott 1997). These processes will have different impacts on species demography and thus must be evaluated separately. Territoriality may occur between members of different species or of the same species (Connell 1983), and it is usually detected by documenting the spatial segregation of the species (Connell 1961, Schoener 1983)

Although territoriality has been observed between sympatric predators, bobcat and fisher home range analysis did not provide any evidence of territorial competition. For example, foxes (*Vulpes fulva*) and coyotes (*Canis latrans*) have been reported to exhibit territorial (interference) competition because of documented spatial segregation (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987). Grey wolves (*Canis lupus*) exclude coyotes from pack territories despite the differences in diets between the species (Carbyn 1982, Thurber et al. 1992). On the other hand, territorial (interference) competition between kit foxes (*Vulpes macrotis*) and coyotes was rejected by White and Garrott (1997) because the species did not segregate spatially. Similarly, Major and Sherburne (1987) concluded that bobcats and coyotes did not interfere with each other because of the lack of spatial segregation of home ranges.

Nearly 40% of bobcat and fisher home ranges overlapped and when this occurred, 40% of fisher home ranges were within bobcat home ranges. Sandell (1989) concluded that individuals whose home ranges overlap by >10% can be said to be non-territorial. Most of the overlap in bobcat and fisher home ranges occurred in the Spider Lake area of CNF. This lowland conifer swamp supported a high population of overwintering deer (Lewis 1990) and dead deer were common. These deer provided food to resident carnivores, and it is this concentrated food supply which apparently caused the overlap in home ranges.

Analysis of separation distances also failed to detect evidence of territoriality or avoidance within overlapping portions of home ranges. Bobcats and fishers appeared to be using their home ranges independently of each other even while within overlapping home ranges. These results were similar to those obtained by Major and Sherburne (1987) and White et al. (1994) who concluded that the observed random-spacing distances provided little evidence of interference competition.

We detected territoriality within each species, however. Fishers maintained separate home ranges from other fishers (both M and F) on the CNF and NNF. Female bobcats also maintained separate home ranges on the SCNR and CNF. Connell (1983) suggested intraspecific territoriality in home ranges indicated intraspecific competition is a stronger influence than interspecific competition. Our results support this hypothesis.

### Consumptive Competition

Consumptive competition occurs when some quantity of resource is consumed by an individual, thereby depriving other individuals of it. For carnivores, the resource most often involved is food, although this need not be the case. Maternal den sites, for example, are resources which are used by both bobcats and fishers (Gilbert et al. 1997) and may be in short supply.

Although direct evidence of territorial or encounter competition can be collected, perhaps all evidence for consumptive competition for food (or other resources) is inferential (Case and Gilpin 1974). One of the primary difficulties in documenting consumptive competition has been demonstrating that the resource sought by both species was in short supply. Thus, in most studies of competition, conclusions have been inferred either from impacts to species demography while in the presence of a competitor or from changes in the utilization distribution of the resource (Ricklefs 1990). If consumptive competition between bobcats and fishers was operating, then all of the demographic parameters investigated in this study should have been lower when bobcats were in the presence of fishers (given the same prey base). However, differences were found in only kitten survival an population growth.

### Encounter Competition

Encounter competition is a second form of interference competition (Schoener 1983) and occurs when one species gains access to increased amount of limited resources by interfering with the ability of its competitor to secure the same resources. When this type of interference occurs in feeding ecology, optimal foraging theory predicts that the poorer competitor will constrict its food habits. If consumptive competition occurs in the absence of interference, then optimal foraging theory predicts that the poorer competitor will broaden its food habits.

Bobcats did not alter food habits while in the presence of fishers. Fishers, on the other hand, consumed a larger biomass of small prey and vegetation where bobcats were abundant. However, in areas where bobcats were scarce, bobcats continued to concentrate on larger prey items, while fishers consumed a broader array of prey, including larger items usually eaten by bobcats. The constriction in fisher diet suggested that bobcats and fishers competed for food, with the bobcat being the dominant competitor (Connell 1983).

**Distinguishing Between Consumptive and Encounter Competition**

There was evidence that bobcats and fishers competed for food resources. However, only 2 of those predictions associated with consumptive competition were found, whereas, the majority of the predictions associated with encounter competition were supported. Population growth and kitten survival were inversely related to fisher abundance. There was no effect of fisher abundance on bobcat adult survival, body condition, or home range, and little effect on bobcat fecundity. Population density was the only parameter tested which did not conform to the predictions under encounter competition. Thus, it is possible that fishers interfered with (or preyed upon) bobcat kittens as hypothesized.

Population modeling implied bobcat kitten survival was low where fishers were common. Kitten survival, although difficult to document, has been shown to be an important variable in bobcat population dynamics, and has been related to reduced prey availability and to increased predation. Bailey (1974) reported that bobcat kitten survival was nearly zero after a crash in prey populations and Rolley (1985) speculated kitten survival during the first 6 months of life was low due to low prey availability. However, Zezulak and Schwab (1979), found that the scarcity of kittens on their study area was due to predation by male bobcats.

If either consumptive or encounter competition occurred, one would expect bobcat populations to grow at a slower rate when fishers were common. Population modeling by WDNR (R. Rolley, personal communication) indicated the bobcat population increased in the northern forest during the 5 years of this study. We found that this increase in population size was reflected in increased bobcat track observations only in S counties, while track count rates remained stable in C counties. This apparent positive rate of population growth in areas where fishers were scarce was consistent with the occurrence of either encounter or consumptive competition.

If bobcat kitten survival was reduced by fishers and if bobcat population growth was lower in areas where fishers were common, one would expect bobcat density to be inversely related to fisher density (Connell 1983). However, this was not the case. The fisher population in northern Wisconsin was expanding during this study, as evidenced by the concentric fisher distribution pattern centered on release sites and the significant relationship between distance from release site and occurrence of fisher tracks on snow-track transects. This distribution of fishers reflects population expansion rather than an established pattern based on prey, habitat factors, or competitors. Fishers have not settled into a distinctive pattern of distribution since their reintroduction and thus there was no relationship detected between fisher density and bobcat density. A positive relationship existed, as demonstrated by positive correlation of relative density, between distributions of bobcats, snowshoe hares, and white-tailed deer; species which have had long residency in Wisconsin. Even though an inverse relationship between bobcat and fisher densities was predicted, the lack of a relationship between their densities was not surprising because of the continued expansion of fisher populations during this study.

If consumptive competition for food resources occurred, and fishers thus deprived bobcats of food, the result should have been reduced fecundity of bobcats. However, if only interference competition occurred, one would expect no relationship between fecundity and fisher abundance. Therefore, this parameter is useful in distinguishing between the 2 types of competition.

Previous studies have shown bobcats to have reduced reproductive output during food shortages. The bobcat reproductive parameter most influenced by food shortages is the percentage of yearling females that become pregnant (Rolley 1985, Knick 1990). Bobcat pregnancy rates, the parameter most influenced by food availability, remained constant for both adults and yearlings between areas. However, we found a significant reduction in bobcat litter size in counties with common fishers but no difference in the litter size of yearling bobcats.

In a review of bobcat survival studies, Fuller et al. (1995) concluded that adult bobcat survival ranges from 0.50–0.67 and averages 0.62 for lightly harvested populations. Survival rates showed little variation across the studies these authors examined, except when poaching or harvests were excessive. Thus, little *a priori* evidence existed that adult survival rates would vary over a wide range of environmental conditions including exposure to potential competitors. We found little variation in adult survival rates and thus support this conclusion. In fact, survival rates calculated from radiocollared bobcats and from life table analysis were nearly identical to those cited by Fuller et al. (1995).

If significant competition deprived bobcats of food there should be less lipid content in bobcat carcasses when fishers are common. However, lipid content of bobcat carcasses was not related to fisher abundance. The only consistent finding was that bobcats had more lipids than fishers. Autumn, when carcasses were collected, is a food-rich time of year. It may be that bobcats and fishers were both well nourished during this time. Evidence of competition may have been apparent if body condition had been evaluated in the late winter or early spring, when food resources for both species may have been reduced.

In summary, bobcats and fishers shared use of space and some food resources, despite overall differences in food habits. Also, we inferred interference competition from the observed constrictions in the diets of fishers while in the presence of bobcats. Finally, we inferred encounter competition, or predation, from the increase in bobcat kitten mortality and reduction in bobcat population growth when fishers were abundant.

**Conservation Implications**

Erdeman et al. (1998) questioned the success of the fisher restoration, contending that this conservation work had unanticipated consequences. They reported fisher predation caused significant nest failure and increased mortality to adult goshawks (*Accipiter gentilis*) so that the population was no longer sustainable. Similar allegations have been made about fisher predation on bobcats that imply an incompatibility between bobcats and fishers.

We found no evidence that bobcats and fishers are incompatible. Bobcat populations in Wisconsin grew during this study despite suggestions of exploitation or encounter competition. Bobcat populations were stationary even in areas common with fishers. Competition between bobcats and fishers was weak and this weak competition should result in a stable coexistence between the species as predicted by Lokta-Volterra competition models (Gotelli 1998).

The restoration of extirpated species is an important aspect of wildlife conservation. In the past decades there have been several restorations of native Wisconsin fauna including the wild turkey (*Meleagris gallopavo*), American marten (*Martes americana*), trumpeter swan (*Olor buccinator*), and gray wolves. Because these restorations have taken place in an environment greatly altered from conditions which existed prior to species' extirpations, the impacts of these restorations on the remaining flora and fauna may be unpredictable. Wildlife managers and restoration biologists are obliged to evaluate the potential impacts that the species restoration efforts may have on present ecosystems in order to minimize unanticipated consequences.

## ACKNOWLEDGMENTS

The Great Lakes Indian Fish and Wildlife Commission has supported this work with funding for research. The North Central Experiment Station of the U.S. Forest Service provided funding for radiocollars and field assistance. The Wisconsin Department of Natural Resources provided unpublished carcass and track count data, which were essential to this project. The University of Wisconsin-Stevens Point collaborated in this work through a Memorandum of Agreement. Under that agreement much of the bobcat telemetry data from the St. Croix National River came from Mathew Lovallo and his thesis (Lovallo 1993).

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# SPATIAL AND RESOURCE OVERLAP OF BOBCATS AND GRAY FOXES IN URBAN AND RURAL ZONES OF A NATIONAL PARK

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***Abstract***: Urbanization reduces and fragments wildlife habitat and threatens the health and natural functioning of populations, communities, and ecosystems. Wide ranging and low density species, such as mammalian carnivores, may be particularly sensitive to the impacts of urbanization. During 1992–95, I studied the ecology of bobcats (*Lynx rufus*) and gray foxes (*Urocyon cinereoargenteus*) in urban and rural zones of Golden Gate National Recreation Area, Marin County, California. Little is known about the interactions between these 2 species or about how these interactions might be affected by humans. In the urban zone, home ranges of bobcats and gray foxes overlapped extensively, although gray foxes used developed areas outside the park and bobcats did not. However, bobcat and fox core areas did not overlap in the urban zone. Gray fox core areas often were adjacent to the park edge or centered around human development within the park. Meadow voles (*Microtus californicus*) dominated the diets of both species in the urban zone. During the wet season when fruits and nuts were not available to foxes, diet overlap was particularly high. A larger predator killed 3 of 8 radiocollared foxes that died in the urban zone. Though bobcats and gray foxes coexist on a broad scale, foxes may avoid bobcat core areas and are at risk to be killed by bobcats. Competition may be intensified in urban landscapes where the amount of suitable habitat is constrained, but foxes may escape competition through the use of developed areas.

***Key words***: bobcat, competition, core areas, diet overlap, gray fox, home range, *Lynx rufus*, overlap, urban wildlife, *Urocyon cinereoargenteus*.

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Interspecific interactions between mammalian carnivores are widespread and can be important on individual, population (Kelly and Durant 2000), and community levels (Crooks and Soule 1999). Competition among carnivores has been studied throughout the world (Schaller 1972, Frame 1986, Johnson et al. 1996). Schoener (1983) specified 6 types of competition in 2 groups: exploitative competition, which included consumptive and preemptive competition, and interference competition, which included territorial, overgrowth, chemical, and encounter competition. While preemptive, overgrowth, and chemical competition generally occur in plants and other sessile organisms, mammalian carnivores compete through consumptive, territorial, and encounter competition. Often intense competition occurs between closely related species because they use similar resources. In carnivores there are many examples of competition between members of the same family, such as Canidae (Johnson et al. 1996), and genus, such as *Canis* (Carbyn 1982, Thurber et al. 1992). However, there are also instances of more distantly related carnivores competing. For example, lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), hyenas (*Crocuta crocuta*), and wild dogs (*Lycaon pictus*) all compete for ungulate prey and for each other's kills in Africa (Schaller 1972, Frame 1986).

In many cases of competition between carnivores, the influence of the superior competitor has been strong enough to affect survival (e.g., kit foxes, *Vulpes macrotis*; Ralls and White 1995), reproduction (e.g., cheetahs, Laurenson and Caro 1994), or spatial distribution (e.g., red foxes, *Vulpes vulpes*; Sargeant et al. 1987) of the weaker, and generally smaller, species. However, many smaller species that may lose in territorial or encounter competition manage to persist in sympatry. The smaller species may find refugia physically, such as in the dens of kit foxes (Cypher and Spencer 1998) and swift foxes (*Vulpes velox*, Kitchen et al. 1999). Further, the smaller species may be able to use resources that are unavailable to the larger competitor, or it may use the common resource more efficiently (Rosenzweig 1966, Durant 1998). This coexistence depends on a heterogeneous environment, both spatially and temporally, so that there are some conditions that favor each species.

One kind of habitat heterogeneity of increasing importance is that produced by humans. Human-altered habitats may have a large impact on carnivore competition and community structure (Buskirk et al. 2000). Species that are better able to coexist with humans may be able to escape pressure from superior competitors through the use of urban, suburban, or agricultural areas or because of human persecution of the larger animal. For example, endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) exist at high densities within the city of Bakersfield where coyotes (*Canis latrans*) are not present (Cypher and Frost 1999). Red foxes may have persisted in central Canada and southeastern Idaho because of coyote harvest and the fox's ability to utilize developed areas (Green and Flinders 1981, Dekker 1983, Voight and Earle 1983). Current research in Illinois shows red foxes persisted given high mortality from coyotes by using urban areas and farmsteads (Gosselink 1999). Cheetahs may also escape lion predation outside national parks in areas where lions are killed and harrassed by humans, but cheetahs are tolerated (Kelly and Durant 2000).

Human-altered landscapes could also increase the competitive pressure on some carnivore species. If the superior competitor is actually more adaptable to human

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presence, then human intrusion into wilderness areas may cause increased competition. For example, coyotes may penetrate deeper into prime lynx (*Lynx canadensis*) habitat through the use of trails and roads (Buskirk et al. 2000). When natural habitat is reduced and fragmented, competition may also be more intense in the smaller patches of habitat that remain, potentially causing local extirpation of inferior competitors if they are not able to persist in the developed portions of the landscape.

In this study, I investigated the relationship between bobcats and gray foxes in urban and rural zones of Golden Gate National Recreation Area. I hypothesized consumptive competition would be relatively unimportant between these species because of the broader diet of the more omnivorous fox. I also hypothesized the larger bobcat would be dominant in any encounter or territorial competition, and that if these kinds of interference competition were present they would be more intense in the urban zone of the park where resources and habitat were more limited.

## STUDY AREA

The study was conducted in Golden Gate National Recreation Area (GGNRA) in Marin County, California. This area is comprised of 30,000 ha of parkland in the San Francisco Bay Area and is one of the most visited parks in the national park system, receiving approximately 14 million visitors per year. Coastal Marin County is characterized by annual grasslands, a chaparral community dominated by coyote bush (*Baccharus pilularis*), riparian woodlands dominated by willows (*Salix* spp.), and oak-bay woodlands dominated by live oaks (*Quercus* spp.) and California bay trees (*Umbellularia california*). Evergreen forests in wetter drainages are dominated by coast redwoods (*Sequoia sempervirens*) and Douglas firs (*Pseudotsuga menziezii*).

I studied bobcats and foxes in 2 areas of GGNRA: the southern part of the park, called the Marin Headlands (hereafter, the urban zone), and the northern part of the park, from the town of Stinson Beach, along Bolinas Lagoon to Olema (hereafter, the rural zone; Fig. 1). The urban site is adjacent to Highway 101, a major 6–8 lane freeway, and the urban areas of Sausalito, Marin City, and Mill Valley. The rural study area, which begins 15 km to the northwest, is 7–17 km from any dense human habitation although there are occasional dwellings and small settlements within the park boundary.

## METHODS

### Live-trapping and Handling

I captured bobcats and gray foxes in homemade box traps (Zezulak 1998) and gray foxes in Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). Both species were chemically immobilized with a 5:1 mixture of ketamine hydrochloride and xylazine hydrochloride injected intramuscularly. I recorded standard body measurements, eartagged animals in both ears with Monel #4 metal eartags (National Band and Tag Co., Newport, Kentucky, USA), recorded sex, and assessed age as juvenile or adult based on dentition.

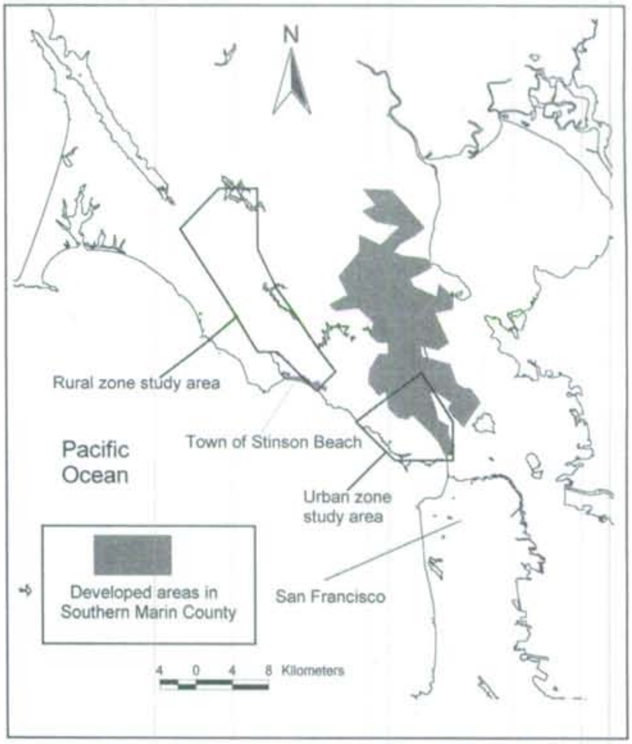


Fig. 1. Study areas in urban and rural zones of Golden Gate National Recreation Area, Marin County, California.

Adults were fitted with Telonics (Telonics, Incorporated, Mesa, Arizona, USA) model 315 (bobcats) and model 225 radiocollars (gray foxes). When animals started to emerge from the effects of the ketamine, an intramuscular injection of yohimbine hydrochloride was given to antagonize the xylazine. When fully recovered, the animal was released at the site of capture. An animal care and use protocol for all capture and handling procedures was approved by the Animal Care and Use Committee at the University of California at Davis (protocol #5328, May 1992).

### Radiotelemetry

Animals were intensively radiotracked for $\geq$12 months (Aug 1992–Mar 1994 in the urban zone and Jan 1994–Mar 1995 in the rural zone). Two day locations and 1 night location were obtained/week for each animal for a total of 38 and 26 months of radiotracking in the urban and rural zones, respectively. Locations were determined using 2 (20%) or 3 (80%) compass bearings obtained with a handheld peak antenna system. I was usually able to get to a point of direct line of sight to the animal (i.e., in the same drainage with the animal or on a ridge above the drainage) before taking bearings. The sites from which I took bearings were pinpointed to $\leq$2–5 m using a Global Positioning System (GPS). I used >360 permanent receiver locations in the urban zone and >460 in the rural zone. Animals, especially bobcats, were also located visually during the day. Visual locations were mapped using compass bearings from 2 known sites or 1 compass bearing and an estimated distance.

Telemetry system accuracy was tested by direct measurement. A field assistant and I placed radiocollars at locations unknown to the other person, but within the home range of a particular animal. The observer then radiotracked the collar as if it were that animal. The locations of the radiocollars were then located with the GPS and the location coordinates were compared to those of the triangulated location. The mean distance between triangulated locations and the test collars was 76.6 m ($n$ = 37, SE = 53.3).

**Home Range and Core Area Estimation**

I computed home ranges and core areas using the minimum convex polygon (MCP) (Hayne 1949) and adaptive kernel methods (Worton 1989). I represented the home range of each animal using a 100% MCP home range and the core area of use (Kaufman 1962) using a 50% adaptive kernel home range.

I computed the percentage of home range overlap for all pairs of bobcats and gray foxes whose home ranges overlapped. For every pair of animals there were 2 data points, one reflecting the percentage overlap of the bobcat on the fox and one of the fox on the bobcat. I also computed the number of different individuals of the other species that overlapped each animal's home range and core area, and the total percentage of each animal's home range and core area that was overlapped by individuals of the other species. I calculated percentage core area overlap for the same animal pairs whose home ranges overlapped. For each species, I tested for differences ($\alpha$ = 0.05) between the sites in home range and core area overlap using a Mann-Whitney U test (SYSTAT, Daniel 1990).

**Food Habits**

I determined bobcat and gray fox food habits with scat analysis. Scats were collected throughout the study period, from fall 1992 through spring 1995 in the urban zone and from fall 1993 through spring 1995 in the rural zone. I determined species by size and shape of scats (Murie 1954) and excluded samples of uncertain origin.

Scats were only collected if they were determined to be recently deposited. Scats were placed in paper bags, air dried, and stored. Before analysis, scats were placed in nylon mesh bags and machine-washed to eliminate the fecal matrix. Scats were allowed to air dry and then hand-separated into hair, bones, and teeth for mammal prey and other diagnostic parts for insect, fruit, bird, reptile, and other food items. I recorded the weight of each group of remains to the nearest 0.1 g. Mammals were identified using a reference collection at the University of California at Davis. Teeth or diagnostic bones were not present in some scats, so remains were classified as small mammal or medium-sized mammal. Insect, fruit, and nut remains were grouped as insects and fruit/nuts for purposes of analysis.

I used 2 methods of food habits analysis: (1) frequency of occurrence, or the number of occurrences of an item divided by the total number of scats and (2) percent fresh weight of prey (%FWP). Frequency of occurrence data were also converted to percentage of occurrence. The weights of hair, bone, and teeth were used in a model based on feeding trials (Kelly 1991, Kelly and Garton 1997) to estimate the fresh weight of each prey item present in each scat. I used program SCAT (Kelly and Garton 1993) to determine %FWP for each item in the diet for which estimators were available.

Diets were determined for both species for each site and for the wet (Nov–Apr) and dry (May–Oct) seasons. I computed diet overlap between species using Pianka's (1973) index of overlap:

$$O_{jk} = \Sigma p_{ij}\, p_{ik} / (\Sigma p_{ij}^{2}\, \Sigma p_{ik}^{2})^{1/2}$$

where $p_{ij}$ is the proportion of item $i$ in the diet of carnivore $j$. The overlap values are a somewhat conservative estimate of overlap because they are computed on many different diet items, including unidentified small mammals and unidentified medium-sized mammals. Though I pooled insects and lagomorphs, I left small mammal food items at the species level to reflect the importance of particular species.

## RESULTS

**Spatial Overlap**

I radiocollared 20 foxes and 10 bobcats in the urban zone and 15 foxes and 12 bobcats in the rural zone. Home ranges of bobcats and gray foxes overlapped in the urban and rural zones (Figs. 2 and 3). In the urban zone, 13 of 17 fox home ranges were overlapped by 1–5 bobcat home ranges ($\bar{x}$ = 2.1, SD = 1.9). Home range overlap of foxes by bobcats was 35–100% in the urban zone ($\bar{x}$ = 63%, SD = 40). In the rural zone, all 10 foxes were overlapped by 1–4 bobcats ($\bar{x}$ = 2.9, SD = 1.2). Home range overlap of foxes by bobcats was 5–100% ($\bar{x}$ = 75%, SD = 36) and 5 fox home ranges were entirely overlapped by bobcat home ranges. All 8 bobcat home ranges in the urban zone were overlapped by 2–11 fox home ranges ($\bar{x}$ = 4.5, SD = 3.0) and overlap ranged from 3–81% ($\bar{x}$ = 40%, SD = 27). The home ranges of the 4 bobcats in the Bolinas area of the rural zone were overlapped by 5–10 fox home ranges ($\bar{x}$ = 7.0, SD = 2.2) and overlap ranged from 7–48% ($\bar{x}$ = 28%, SD = 17). Home range overlap did not differ between sites for either bobcats ($U_{11}$ = 13.0, $P$ = 0.610) or foxes ($U_{36}$ = 108.5, $P$ = 0.231).

Although core areas overlapped extensively in the rural zone (Fig. 5), little core area overlap between bobcats and foxes existed in the urban zone (Fig. 4). In the urban zone only 4 fox core areas were overlapped by bobcat cores ($\bar{x}$ = 0.29, SD = 0.75) and average overlap was 4% (SD = 9). Urban zone bobcat core areas were overlapped by 1–3 fox core areas ($\bar{x}$ = 0.75, SD = 1.04) and overlap ranged from 0–7% ($\bar{x}$ = 3%, SD = 5). In the rural zone, 0–2 bobcat core areas ($\bar{x}$ = 0.90, SD = 0.74) overlapped fox core areas with overlap ranging from 0–100% ($\bar{x}$ = 45%, SD = 39), and 0–3 fox cores ($\bar{x}$ = 2, SD = 2) overlapped bobcat cores by 0–28% ($\bar{x}$ = 16%, SD = 13). Though core area overlap of foxes on bobcats did not differ in the rural zone ($U_{11}$ = 26.0, $P$ = 0.078), core area overlap of bobcats on foxes was greater in the rural zone ($U_{36}$ = 138.0, $P$ = 0.002).

**Diet Overlap**

I analyzed 325 bobcat scats ($n$ = 188 in the urban zone and $n$ = 137 in the rural zone, Table 1) and 247 gray fox scats ($n$ = 132 in the urban zone and $n$ = 115 in the rural zone, Table 2). Meadow voles were the most important items in both species' diets. Urban zone overlap between bobcat and gray fox diets was 0.61 for percent occurrence ($n$ = 14 items) and 0.92 for %FWP ($n$

Table 1. Diets (% fresh weight of prey and % occurrence) of bobcats in urban and rural zones of Golden Gate National Recreation Area, Marin County, California, 1992–95.

| | Urban zone | | Rural zone | | Urban zone, wet season | |
|---|---|---|---|---|---|---|
| | % FWP | % Occurrence | % FWP | % Occurrence | % FWP | % Occurrence |
| Meadow vole (*Microtus californicus*) | 67.5 | 50.1 | 53.3 | 42.4 | 65.6 | 51.7 |
| Lagomorphs (*Sylvilagus* and *Lepus*) | 13.3 | 7.8 | 7.9 | 7.0 | 10.7 | 7.0 |
| Pocket gopher (*Thomomys bottae*) | 8.7 | 13.8 | 17.9 | 21.8 | 10.9 | 16.3 |
| Mule deer (*Odocoileus hemionus*) | 4.8 | 2.2 | 15.1 | 7.4 | 8.1 | 4.1 |
| White-footed mouse (*Peromyscus maniculatus*) | 1.7 | 8.3 | 1.5 | 4.8 | 1.5 | 7.6 |
| Dusky-footed woodrat (*Neotoma fuscipes*) | 1.7 | 1.8 | 1.8 | 2.6 | 1.4 | 1.7 |
| Unknown med. mamm. | 1.2 | 2.5 | 1.1 | 2.2 | 1.5 | 2.9 |
| Birds | 0.7 | 3.4 | 0.6 | 2.6 | 0.1 | 2.3 |
| Insects | 0.1 | 3.1 | 0.1 | 2.2 | 0.1 | 2.9 |
| Harvest mouse (*Reithrodontomys megalotis*) | 0.1 | 0.6 | 0.1 | 0.4 | 0.2 | 0.6 |
| Unknown small mamm. | 0.0 | 0.0 | 0.4 | 2.6 | 0.0 | 0.0 |
| Reptiles | | 3.1 | | 3.5 | | 2.3 |

Table 2. Diets (% fresh weight of prey and % occurrence) of gray foxes in urban and rural zones of Golden Gate National Recreation Area, Marin County, California, 1992–95.

| | Urban zone | | Rural zone | | Urban zone, wet season | |
|---|---|---|---|---|---|---|
| | % FWP | % Occurrence | % FWP | % Occurrence | % FWP | % Occurrence |
| Meadow vole (*Microtus californicus*) | 46.1 | 21.4 | 35.8 | 22.7 | 47 | 29.3 |
| Fruit/nuts | 14.3 | 19.0 | 9.4 | 21.0 | 4.1 | 10.6 |
| Unknown small mamm. | 7.9 | 6.8 | 5.9 | 9.7 | 9.8 | 8.9 |
| Insects | 5.9 | 23.1 | 4.6 | 23.5 | 3.2 | 23.6 |
| Unknown med. mamm. | 5.7 | 2.0 | 3.3 | 3.4 | 10 | 4.1 |
| Lagomorphs (*Sylvilagus* and *Lepus*) | 4.7 | 2.0 | 11.1 | 4.2 | 6.7 | 3.3 |
| Mule deer (*Odocoileus hemionus*) | 4.6 | 0.7 | 15.9 | 1.3 | 8.2 | 1.6 |
| Birds | 3.7 | 5.4 | 2.9 | 2.9 | 3.7 | 6.5 |
| White-footed mouse (*Peromyscus maniculatus*) | 2.3 | 2.4 | 6.0 | 3.8 | 3.4 | 4.9 |
| Pocket gopher (*Thomomys bottae*) | 2.3 | 2.0 | 1.0 | 0.4 | 3.0 | 3.3 |
| Dusky-footed woodrat (*Neotoma fuscipes*) | 2.3 | 1.0 | 3.0 | 1.3 | 0.7 | 0.8 |
| Harvest mouse (*Reithrodontomys megalotis*) | 0.1 | 0.7 | 1.2 | 0.8 | 0.2 | 1.6 |
| Reptiles | | 1.0 | | 1.7 | | 0.8 |
| Human food (Trash, etc.) | | 2.0 | | 1.3 | | 0.8 |

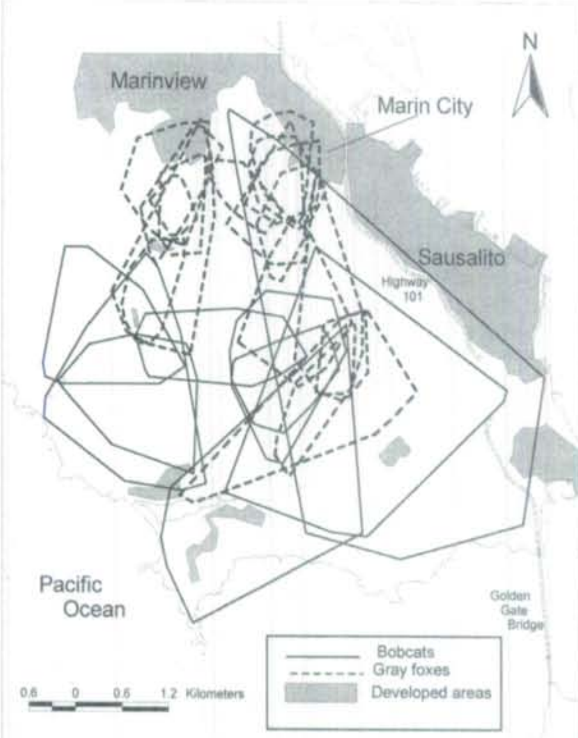


Fig. 2. Minimum convex polygon home ranges (100%) of bobcats and gray foxes in the urban zone of Golden Gate National Recreation Area, Marin County, California.

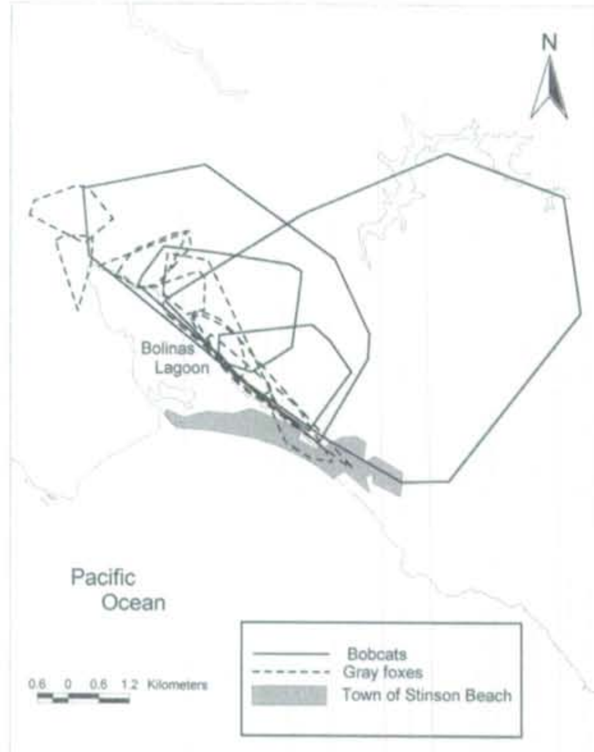


Fig. 3. Minimum convex polygon home ranges (100%) of bobcats and gray foxes in the rural zone of Golden Gate National Recreation Area, Marin County, California.

= 12 items, omitting reptiles and human items such as trash). Rural zone dietary overlap was 0.56 for percent occurrence ($n$ = 16 items) and 0.90 ($n$ = 13 items, omitting snakes, dog food, and human items) for %FWP. In the urban zone, wet season overlap was 0.75 for percent occurrence ($n$ = 15 items) and 0.95 for %FWP ($n$ = 12 items, omitting reptiles, trash, and bats). In the rural zone, wet season overlap was 0.55 for percent occurrence ($n$ = 16 items) and 0.90 for %FWP ($n$ = 13 items, omitting reptiles, dog food, and trash).

**Potential Intraguild Predation**

Eight of 20 radiocollared foxes died in the urban zone and 3 of these were killed by a larger carnivore, although none of them was eaten. Necropsy and field evidence could not identify the carnivore responsible. No foxes were killed by other predators in the rural zone. In June 1992, just before the study began, I observed a bobcat chasing a gray fox across a rock outcropping above a fire road. The bobcat stopped to look at a vehicle and the fox continued to sprint away out of sight. The area was later frequented by 2 radiocollared male bobcats.

## DISCUSSION

Bobcats and gray foxes were abundant in both the urban and rural zones of Golden Gate National Recreation Area, and on a landscape scale these carnivores clearly coexisted. The high degree of interspecific home range overlap at both study sites also indicates that these species regularly utilize the same space. In addition to the high degree of overlap on a broad scale, closer examination revealed that individual bobcats and gray foxes interact and may directly compete for resources.

In the urban zone, bobcat core areas did not overlap those of foxes. Past studies showing interspecific territoriality between carnivores have found little spatial overlap at all between competing species, and the authors have inferred that the smaller species is avoiding the larger one (Sargent et al. 1987, Harrison et al. 1989). In this case, it may be that gray foxes tolerate spatial overlap on the periphery of their home range but not in their areas of most concentrated activity. A similar relationship of home range overlap but little core area overlap was found between coyotes and wolves in Montana (Arjo and Pletscher 1999). Young foxes would likely be especially vulnerable to attack from bobcats, and so gray fox pairs would likely choose denning areas that were less frequented by potential competitors. One of the few published accounts of a bobcat-gray fox interaction details a fox pair harassing and chasing a bobcat that was near their den (Dudley 1976).

Dietary overlap between bobcats and gray foxes as measured by percent occurrence was low in both zones because of omnivorous fox diets. However, fox diets varied considerably seasonally, with fruit occurring predominantly during the dry season. Bobcat diet was focused very heavily on a single prey item, the meadow vole (*Microtus californicus*). Voles were also the most important mammalian prey for foxes by both measures. Therefore, during the wet season dietary overlap was higher between the species because of the increased reliance on voles by foxes. Overlap values for the %FWP

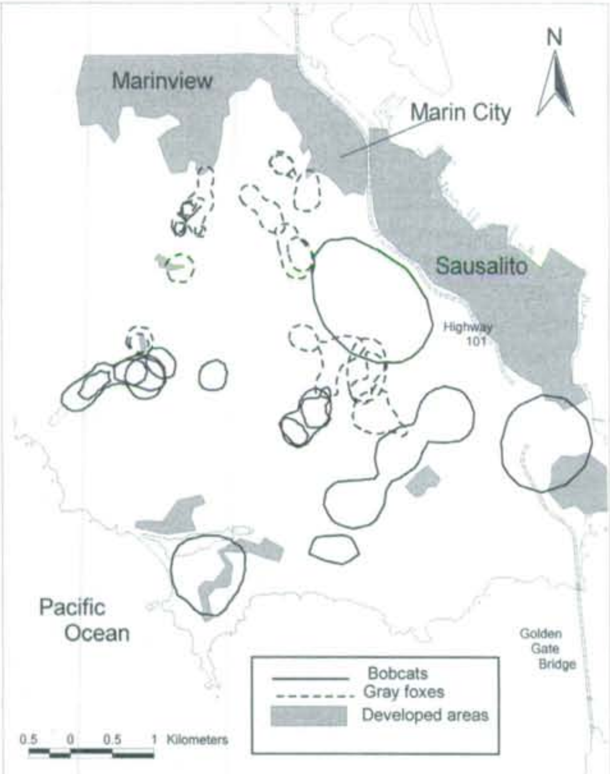


Fig. 4. Adaptive kernel core areas (50%) of bobcats and gray foxes in the urban zone of Golden Gate National Recreation Area, Marin County, California.

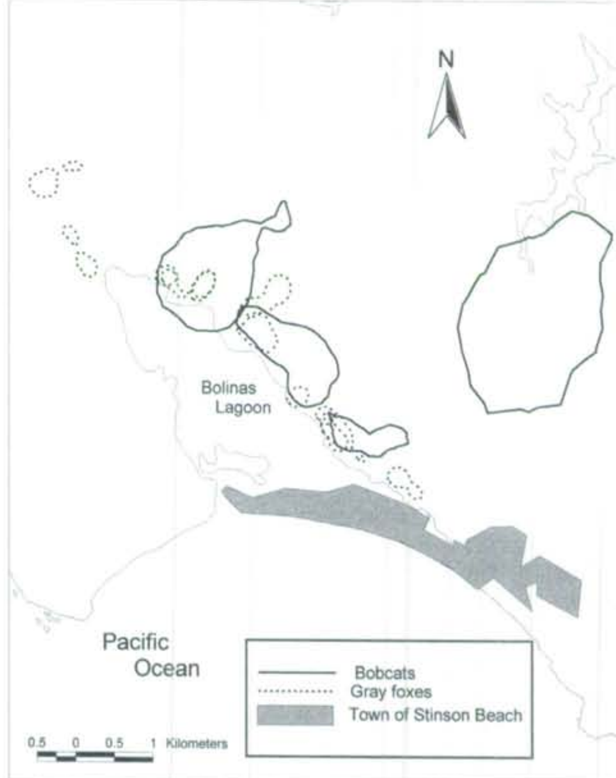


Fig. 5. Adaptive kernel core areas (50%) of bobcats and gray foxes in the rural zone of Golden Gate National Recreation Area, Marin County, California.

diets were higher than those for the percent occurrence diets because of low values for fruit and insects and the large percentage of fresh weight represented by voles in both species' diets.

It may be that, in spite of high dietary overlap during the winter, consumptive competition did not occur between bobcats and foxes. Competition over a resource requires that the resource is scarce or at least limiting, and voles appeared to be abundant. There are other examples of very high resource overlap in sympatric carnivores that did not appear to be competing. For example, Witmer and DeCalesta (1986) studied coyote and bobcat populations in Oregon that were both relying almost entirely on mountain beaver (*Aplodontia rufa*) with diet overlap values >0.97. However, many small mammal populations frequently cycle with great amplitude (Krebs and Myers 1974, Lidicker 1988), and competition could occur during the trough of a cycle. Studies of lynx in Canada have found that interspecific competition in the form of killing and eating other carnivores (i.e., intraguild predation; Polis et al. 1989) such as red foxes increases markedly during the low period of the snowshoe hare cycle (Stephenson et al. 1991, O'Donoghue et al. 1995), although other studies have reported that many red fox kills by lynx are uneaten (Sunde et al. 1999). However, central coastal California is very different from high latitude Canada and microtine cycles tend to be more common and more dramatic at high latitudes (Hanski et al. 1991), so perhaps bobcats and foxes can coexist over the long term on high-density vole populations.

Regarding encounter competition, gray foxes in this study, particularly in the urban zone, are at risk of being attacked and killed by other carnivores. Three of the 8 dead foxes in the urban zone were killed, though not eaten, by another predator. While it is difficult to unequivocally suspect bobcats in these cases, bobcats were definitely the most abundant larger carnivore in the urban zone and I observed a bobcat chasing a fox on one occasion. Other instances of bobcats attacking or harassing gray foxes have been reported (Trapp and Hallberg 1975, Dudley 1976), and 2 of 11 gray foxes killed by predators in southern California were killed by bobcats (Fedriani et al. 2000). Bobcats also attacked and killed endangered San Joaquin kit foxes and were the leading cause of mortality in one study (Disney and Speigel 1992). The closely related lynx has also been known to attack and kill red foxes (Stephenson et al. 1991, Sunde et al. 1999). Though coyotes are a significant mortality factor for gray foxes in southern California (Fedriani et al. 2000) and for other small foxes such as kit foxes (Ralls and White 1995) and swift foxes (Sovoda et al. 1998, Kitchen et al. 1999), coyotes had been previously extirpated from the urban zone and were just beginning to reenter the area during the study (S. Riley, personal observation). Presently, coyotes appear to be much more abundant in southern Marin County (S. Riley, personal observation), but their potential effects on the gray fox population are unknown.

Interactions between bobcats and gray foxes seemed to be more intense in the urban zone than in the rural zone. Home ranges and core areas overlapped extensively in the rural zone, whereas in the urban zone there was essentially no interspecific overlap of core areas. Certainly not every animal was radiocollared at either site, but uncollared foxes that were seen or trapped in the urban zone were in areas not within bobcat core areas. Further, although predators caused mortalities of urban zone foxes, no such mortalities were reported in the rural zone. Finally, dietary overlap was higher in the urban zone than in the rural zone, especially during the wet season.

The increase in competitive pressure in the urban zone may be related to its smaller area and the hard constraints of development on the east side and the ocean on the west side. In the rural zone, bobcat home ranges are much larger (Riley 1999), which would likely lead to less intense use of the home range and fewer interspecific encounters. The rural zone also included more forested habitat and less grassland, which may have allowed the smaller fox more cover and probably contributed to a decreased reliance on voles by both species. Voles were more important in the diet of urban zone bobcats by both percent occurrence and %FWP. In the urban zone, voles were present in 90% of scats while in the rural zone voles were present in 70% of scats.

The difference in bobcat and fox spatial use in the urban zone was certainly associated with the use of different habitats. In the urban zone, adult female bobcats placed core areas in grasslands near stream courses. Alternately, fox core areas existed in areas of oak woodland and thick coastal chaparral. Foxes also used developed areas in a way that bobcats did not. No bobcats left the natural habitats of the park to enter developed areas outside the park and adult female bobcats did not even utilize areas adjacent to the urban edge (Riley 1999). Conversely, 10 of 20 radiocollared foxes were located in developed areas outside the park and another 4 foxes regularly utilized developed areas within the park such as barns and residences. Three of the other 6 foxes had home ranges adjacent to the urban edge (Riley 1999).

Gray foxes probably do not utilize developed areas solely in order to escape from competitors, but also to take advantage of resources such as ornamental fruits, trash, pet food, and residents who regularly feed wildlife. However, the use of developed areas may also allow foxes to escape competition with larger carnivore species, such as bobcats, that are less able to adapt to humans. Peterson (1988) suggested that humans may sometimes act as a keystone species in carnivore communities by eliminating certain species and thereby allowing inferior competitors to persist. While competition between bobcats and gray foxes may not be so intense as to drive foxes to local extirpation, use of developed areas may allow foxes to maintain higher densities when sympatric with bobcats.

## ACKNOWLEDGMENTS

I thank the Golden Gate National Recreation Area for extensive logistical and financial support throughout the field portion of this work and J. Howell, C. Schonewald, and D. Van Vuren for encouragement and assistance both in the field and after. I thank Earthwatch for financial support, 18 teams of Earthwatch volunteers for their assistance and enthusiasm, and B. McKeon and G. Brooks for their excellent and tireless work in the field. S. Skartvedt and M. Semenoff-Irving provided indispensable training and help with geographic information systems software and the various GPS units. I thank J. Hadidian for introducing me to urban wildlife, carnivores, and the right attitude about animals and research. I thank E. Kelley, C. Bromley, and P. Roby for comments on earlier versions of this paper and C. Nielsen and A. Woolf for excellent honing of the text.

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# BOBCAT HABITAT USE RELATIVE TO HUMAN DWELLINGS IN SOUTHERN ILLINOIS

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***Abstract***: Wildlife and humans are in increasing contact as human populations expand in rural areas. Although certain species are faring well given these conditions, it is unclear whether more sensitive species will respond favorably to increased human prevalence. Bobcats (*Lynx rufus*) are secretive predators that are generally thought to avoid humans; however, because most bobcat studies have been conducted in areas of low human population density, the influence of human activities other than harvest on bobcats remains unknown. We addressed this paucity in the literature by assessing habitat use by 19 adult bobcats (7 M, 12 F) relative to human dwellings in southern Illinois, a region dominated by rural landscapes and high human population density (17.8 persons/km$^2$) relative to most bobcat studies. Because forest cover types were most prevalent and preferred by bobcats on the study area ($P < 0.0200$), we constrained location-based analyses to dwellings within forest cover types only ($n = 198$). We established zones of potential human influence (i.e., circular buffers of diameter 384 m) around dwellings based on the mean distance from the nearest bobcat location ($n =$ 1,648) to each dwelling and created buffers of the same size for 198 random locations. More bobcat locations ($P <$ 0.0001) were found in random areas than in zones of influence surrounding dwellings. Further, proportionately more ($t_{18} =$ -2.15, $P = 0.0425$) structures were found within home ranges ($\bar{x}$ ratio of dwellings to home range size = 2.8, SD = 1.9) than core areas ($\bar{x}$ ratio of dwellings to core area size = 1.9, SD = 1.8). Although bobcats appear to avoid human presence and are subjected to relatively high rates of human-caused mortality, bobcat populations are growing in southern Illinois. However, if humans continue to populate non-metropolitan areas at increasing rates, bobcat populations may be adversely affected. Regardless, managers can take a conservative approach by focusing on areas of rugged terrain or public land ownership for bobcat conservation because these places will likely remain refugia for bobcats.

***Key words***: bobcat, habitat use, human dwellings, human-wildlife interactions, *Lynx rufus*.

Wildlife and humans are in increasing contact as human populations expand (Adams and Leedy 1991). Population growth in the United States was about 16% between 1980 and 1995 (Frey and Johnson 1998:95). Further, population growth in non-metropolitan areas during the 1990s (5.1%) almost doubled that of the 1980s (2.7%). Although certain species have fared relatively well given these conditions (e.g., white-tailed deer [*Odocoileus virginianus*], Halls 1984), it is unclear how more sensitive species will respond to increased human presence.

Bobcats (*Lynx rufus*) are secretive carnivores that thrive in a variety of habitats and are generally thought to avoid humans (Anderson 1987). However, bobcats have not been studied in areas of relatively high human densities; instead, they usually were studied in relatively undeveloped publicly-owned or protected settings (e.g., Bailey 1974, Berg 1979, Hamilton 1982). Although the numerical (e.g., removal of individuals; Heisey and Fuller 1985, Rolley 1985) and functional effects (e.g., changes in social organization; Litvaitis et al. 1987, Lovallo and Anderson 1995) of harvest on bobcat populations have been described, the influence of human activity other than harvest on bobcats remains essentially unknown.

During 1995–99, we studied ecology of unexploited bobcats in southern Illinois, a region characterized by rural landscapes and relatively high human population densities (Woolf and Nielsen 1999) that provided an excellent opportunity to gain insight into the influence of human presence on bobcats. Specifically, we assessed habitat use by adult bobcats relative to human dwellings (i.e., representative areas of human activity) and determined whether bobcats avoided dwellings in areas of preferred habitat.

## STUDY AREA

We studied bobcats within a portion of a 1,000-km$^2$ study area in Jackson and Union counties, southern Illinois (Woolf and Nielsen 1999:8). Land use/land cover (Luman et al. 1996) consisted primarily of closed-canopy mixed hardwood forests (66%), dominated by white oak (*Quercus alba*), black oak (*Q. rubra*), and hickory spp. (*Carya* spp.); rural grasslands (16%); and cropland (8%) characterized by corn and soybeans. Streams were abundant on the landscape (stream density = 1.1 km/km$^2$). Elevation ranged from 92–316 m, with an average slope of 1.4°. The study area also was characterized by a relatively high level of human influence, resulting in a patchy landscape with a high interspersion of land cover types. Human population density was 17.8 persons/km$^2$ and road densities were 1.4 km/km$^2$. Bobcats were a state-threatened species in Illinois until 1999 and have been protected from harvest statewide since 1971.

## METHODS

### Capture and Radiotelemetry

Bobcats were captured primarily on privately-owned lands during November–March 1995–99 with either cage-type traps constructed of galvanized wire mesh (38 x 38 cm x 90 cm) or padded number 3 Soft-catch®

(Woodstream Co., Lititz, Pennsylvania, USA) foot-hold traps. Traps were baited with meat from a variety of wild birds and mammals; commercial bobcat lures and visual attractants were frequently used in combination.

Captured bobcats were chemically immobilized for handling with a combination of ketamine hydrochloride (HCl) and xylazine HCl (both in 100 mg/mL concentration solution). The drugs were premixed in a solution of 90 mg ketamine and 10 mg xylazine/mL and administered intramuscularly at a target dose of about 13 mg ketamine/kg estimated body mass. We used a pole-syringe to inject the drug mixture into the hip or thigh muscle of bobcats in foot-hold traps. Most bobcats in cage traps were constrained in 1 end with a device constructed of reinforcing rods and injected with a hand-syringe.

Bobcats were sexed, weighed, measured, and classified as adults ($\geq$2 yr) or juveniles based on size, mass (bobcats <5 kg were considered juveniles), and condition of dentition. We also examined bobcats for injuries, ectoparasites, and overall physical condition. Capture and handling procedures were conducted in accordance with a protocol approved by the Southern Illinois University at Carbondale Institutional Animal Care and Use Committee (Southern Illinois University at Carbondale Animal Assurance #A-3078-01) and under provisions of Illinois Endangered Species Permit #95-14S issued to the second author.

We fitted bobcats with Telonics (Mesa, Arizona, USA) model 315-S6A and Wildlife Materials (Carbondale, Illinois, USA) model HLPM-2140M radiocollars equipped with mortality sensors. Collars weighed 120–130 g; expected transmitter life was 17 and 20 months for Telonics and Wildlife Materials units, respectively. We used standard ground and aerial radiotelemetry techniques to track bobcats (White and Garrott 1990). One vehicle, a TS-1 scanner (Telonics, Mesa, Arizona, USA), hand-held 2- or 3-element yagi antennas, and a compass were used for ground tracking. Two-element yagi antennas mounted on the wing struts of a Cessna 172 aircraft or on the skid of a Bell Long Ranger II helicopter were used for aerial telemetry.

We determined point locations (Universe Transverse Mercator coordinate system) of bobcats from radiotelemetry, capture, and visual locations. Most (91%) locations were obtained by taking $\geq$2 bearings from bearing stations <2 km from bobcats. Less than 20 min elapsed between first and last bearings for 94% of all locations. We used the program LOCATEII (Nams 1990) to estimate locations according to the maximum likelihood estimator (Lenth 1981) and to calculate bearing error ($n$ = 200, $\bar{x}$ = 4.16°, SD = 3.00) and error polygons ($n$ = 200, $\bar{x}$ = 1.59 ha, SD = 1.82; Springer 1979).

**Bobcat Habitat Use Relative to Human Dwellings**

We used locations ($n$ = 1,648), home ranges, and core areas of 19 adult bobcats (7 M, 12 F) with >30 locations for habitat use analysis. The number of locations per bobcat averaged 89.6 (SD = 47.9). Program RANGES V (Kenward and Hodder 1996) was used to estimate 100% home ranges and 50% core areas (km$^2$) using the minimum convex polygon estimator (Mohr 1947). We analyzed habitat use by bobcats relative to 954 human dwellings within bobcat home ranges. Dwellings were obtained from county 911 data (S. Sylvester, Jackson County Illinois, personal communication) or were manually digitized from United States Geological Survey Digital Orthophoto Quadrangles. We derived land cover information from Landsat TM imagery at 28.5 m$^2$ pixel resolution (Luman et al. 1996) reclassified from the original 23 cover classes into the following 8 aggregations: urban, transportation (i.e., roads and railroads), agriculture, grass, woods, open water, streams, and marsh. All digital data were stored and analyzed in a geographic information system (ArcView 3.2; Environmental Systems Research Institute Corporation, Redlands, California).

We determined cover types associated with the study area and bobcat locations, and used chi-square (Neu et al. 1974) to test the null hypothesis of no differences ($\alpha$ = 0.05) in cover-type affiliations between bobcat locations and the study area. Other studies have indicated that bobcats prefer forest cover types (Anderson 1987). Therefore, to control for potential habitat preferences, we concentrated further analyses on dwellings and random areas within the most prevalent and preferred cover type (i.e., forest) only. We established circular zones of potential human influence around dwellings and random points and determined proportional land cover within each zone. The 1.2-km$^2$ circular zones were based on the mean distance from the nearest bobcat location to each dwelling ($\bar{x}$ diameter = 384 m, SD = 298); we reasoned this buffer size encompassed a liberal range of human influence. We retained zones of human influence ($n$ = 198) with $\geq$70% forest cover (i.e., matching the proportional habitat use by bobcats) and selected an equal number of random zones containing $\geq$70% forest cover and no dwellings. The number of bobcat locations within zones of influence and random areas was then calculated; chi-square tests were used to test the null hypothesis of no difference in number of locations between the 2 areas.

We also examined the number of human dwellings within bobcat home ranges versus core areas. Because different use-area sizes among individuals would bias results, we calculated ratios of number of dwellings to use-area size for each individual. T-tests were then used to test the null hypothesis of no difference in mean ratios of number of dwellings to use-area size between home ranges and core areas.

## RESULTS

Cover types used by bobcats differed from cover types available on the study area ($\chi_1^2$ = 6.17, $P$ < 0.0200). Bobcats used less grass and transportation cover, but more agriculture and forest cover, than available on the study area (Table 1). Random areas contained more bobcat

Table 1. Mean proportional cover types associated with the study area and bobcat locations in southern Illinois, 1995–99.

| | Cover type proportions | |
|---|---|---|
| Cover type | Study area | Locations |
| Urban | — | — |
| Transportation | 0.05 | 0.03 |
| Agriculture | 0.08 | 0.11 |
| Grass | 0.15 | 0.12 |
| Forest | 0.65 | 0.70 |
| Water | 0.03 | — |
| Streams | 0.03 | 0.03 |
| Marsh | 0.01 | 0.01 |

locations ($n = 656$, $\chi_1^2 = 80.36$, $P < 0.0001$) than zones of influence surrounding dwellings ($n$ locations = 369).

Home range and core area sizes ranged from 4.8–80.3 and 0.4–11.2 km², respectively (Table 2). Number of dwellings per use-area ranged from 4–559 and 0–29 for home ranges and core areas, respectively (Table 2). Proportionately more dwellings ($t_{18} = -2.15$, $P = 0.0425$) were within bobcat home ranges ($\bar{x}$ ratio of dwellings to home range size = 2.8, SD = 1.9) than core areas ($\bar{x}$ ratio of dwellings to core area size = 1.9, SD = 1.8).

## DISCUSSION

Human dwellings provided a surrogate for human activities that may cause bobcats to avoid areas inhabited by humans. We found more bobcat locations in random areas than zones of influence surrounding dwellings, which implies bobcats may avoid human activities. For this analysis, we controlled for the confounding effect of habitat preference by focusing on dwellings within forest, the most prevalent and preferred cover type on the study area.

Bobcat core areas contained proportionately fewer dwellings than were present within home ranges. We previously found habitat use did not differ between home ranges and core areas for either males or females (C. Nielsen, unpublished data); hence, core area placement was probably more influenced by social interactions than habitat use (Nielsen and Woolf, in review). Clearly, myriad factors influence spatial use in bobcats (Anderson 1987); however, our results imply bobcats may select core areas to provide retreat from human activity.

Potential negative influences of human activities on bobcats are manifold. First, landscape manipulation to less favorable cover types may occur with increased human density. As humans develop rural areas, highly-suitable forest cover will likely be removed and replaced with lawns, golf courses, and pavement; thereby reducing prey densities and suitable denning areas. Second, human

Table 2. Size (km²) of and number of human dwellings within minimum convex polygon home ranges and core areas of bobcats in southern Illinois, 1995–99.

| | Home range | | | Core area | | |
|---|---|---|---|---|---|---|
| Bobcat | No. dwellings | Size | Ratio | No. dwellings | Size | Ratio |
| 1 | 46 | 24.1 | 1.9 | 2 | 3.6 | 0.6 |
| 5 | 67 | 14.5 | 4.6 | 9 | 2.9 | 3.1 |
| 8 | 29 | 12.9 | 2.2 | 0 | 1.8 | 0.0 |
| 9 | 90 | 45.2 | 2.0 | 12 | 11.2 | 1.1 |
| 13 | 109 | 34.2 | 3.2 | 29 | 4.4 | 6.6 |
| 14 | 73 | 48.8 | 1.5 | 10 | 6.3 | 1.6 |
| 15 | 43 | 26.3 | 1.6 | 2 | 8.9 | 0.2 |
| 17 | 559 | 80.3 | 7.0 | 19 | 9.5 | 2.0 |
| 32 | 42 | 16.9 | 2.5 | 5 | 4.2 | 1.2 |
| 33 | 60 | 19.1 | 3.1 | 4 | 2.5 | 1.6 |
| 36 | 19 | 38.0 | 0.5 | 3 | 5.9 | 0.5 |
| 47 | 135 | 41.8 | 3.2 | 16 | 3.3 | 4.9 |
| 48 | 36 | 9.5 | 3.8 | 4 | 1.6 | 2.5 |
| 49 | 9 | 8.1 | 1.1 | 1 | 2.0 | 0.5 |
| 57 | 4 | 4.9 | 0.5 | 0 | 0.4 | — |
| 58 | 71 | 9.3 | 7.6 | 5 | 1.3 | 3.8 |
| 60 | 7 | 7.1 | 1.0 | 1 | 2.1 | 0.5 |
| 68 | 15 | 4.8 | 3.1 | 3 | 1.5 | 2.0 |
| 72 | 11 | 5.1 | 2.1 | 2 | 0.6 | 3.4 |

activities near dwellings (e.g., all-terrain vehicle operation or mowing) may disrupt bobcat behavior. Third, road densities will likely increase as human densities grow. These changes will certainly have a negative influence on bobcats; indeed, vehicles caused 11 of 18 bobcat mortalities in our study (A. Woolf, unpublished data). Finally, increasing human densities may result in more accidental mortalities via hunting or trapping (e.g., Lovallo and Anderson 1996). We confirmed 2 instances of bobcats killed accidentally by trappers (Woolf and Nielsen 1999) and 1 bobcat killed by a car had been previously shot. Further, the unexplained disappearance of 3 bobcats from the study area may have been caused by humans and concealed via radiocollar destruction.

Although bobcats may avoid human activities and despite the fact that humans are the primary cause of mortality, the bobcat population in southern Illinois has increased in abundance and distribution (Woolf and Nielsen 1999). Almost 30 years of harvest restriction have allowed bobcat populations to increase from levels warranting their status as State Threatened (Woolf et al. 2000) to relatively high densities (0.27/km$^2$; A. Woolf, unpublished data). Bobcat survival rates of >80% are among the highest recorded (Woolf and Nielsen 1999). Critical life-history requisites are not limiting, as evidenced by only 1 confirmed natural mortality; cachexia due to stomach obstruction from a large hairball. Further, a separate database of bobcat necropsies (A. Woolf, unpublished data) confirmed that debility from either infectious disease or malnutrition was highly uncommon (Woolf and Nielsen 1999).

Several instances were confirmed of bobcats using human structures, indicating that human activities may occasionally be beneficial to bobcats. For example, we documented one instance of a female bobcat having a litter in a barn. Further, we received several complaints of bobcat depredation of pen-raised birds, and captured 2 bobcats in bird-raising facilities. We also captured several bobcats within 100 m of human structures.

## MANAGEMENT IMPLICATIONS

Although bobcats appear to avoid human presence and are subjected to relatively high rates of human-caused mortality, bobcat populations are growing in southern Illinois. Our study area contained relatively high bobcat and human densities; however, we may not have yet reached the critical point at which human influence is a more severe limiting factor to bobcat populations. Conjecture about future trends in non-metropolitan development is questionable given the unpredictability of human migration and its manifold influences (Frey and Johnson 1998). However, if humans continue to populate non-metropolitan areas at increasing rates, bobcat populations may be adversely affected. Regardless, managers should take a conservative approach by focusing on areas of rugged terrain or public land ownership for bobcat conservation. Because human influence may continue to be limited in these areas, they will likely remain refugia for bobcats over the long term.

Finally, we propose that researchers consider human influence during studies of bobcat ecology. Our analysis represents a simple approach that provides a first look at bobcat-human interactions. A more complex analysis involving direct comparisons of survival and habitat use of bobcats in areas of high versus low human influence within the same region would likely provide more convincing evidence regarding human influence on bobcats.

## ACKNOWLEDGMENTS

This study was funded through the Federal Aid in Wildlife Restoration program (Project W-126-R, Status of the Bobcat in Illinois), the Cooperative Wildlife Research Laboratory at Southern Illinois University at Carbondale, and the Division of Wildlife Resources, Illinois Department of Natural Resources, cooperating. We thank B. Bluett of the Illinois Department of Natural Resources for support and encouragement. C. Harden provided Jackson County 911 data. C. Greene, J. Kolowski, M. Krecja, C. Schieler, C. Vincent, and M. Woodruff provided field assistance with trapping and radiotelemetry. We thank all cooperating trappers and landowners for their assistance and access to property. J. Roseberry, M. Nicholson, and J. Kolowski provided timely reviews of the manuscript.

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# SPATIO-TEMPORAL RELATIONSHIPS AMONG ADULT BOBCATS IN CENTRAL MISSISSIPPI

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***Abstract:*** Bobcats (*Lynx rufus*) are considered territorial and previous studies have indicated that intersexual overlap in space use occurs, but intrasexual overlap of females is rare. Most researchers have reported a lack of social interactions among bobcats except during mating, suggesting that bobcats are solitary. However, inferences regarding spatial and temporal relationships have been based on small sample sizes and studies of short duration. We radiomonitored 58 (20 M, 38 F) adult bobcats from 1989–97, documenting 33, 117, and 158 instances of home range overlap for males, females, and male-female combinations, respectively. Neighboring males exhibited greatest overlap during winter, whereas overlap among females was similar seasonally. Males and females exhibited greatest overlap during breeding periods. Intrasexual core area overlap was negligible during all seasons. Neighboring males were located rarely within <100 m of each other and frequently exhibited negative interactions, whereas females with overlapping home ranges and core areas were frequently located closer together than expected. Overlap averaged 20% seasonally for neighboring males and females, suggesting little territoriality at the home range level, but most core areas were maintained exclusively. Our findings suggest neighboring males and females likely use areas outside of core areas close to one another, but that movement of 1 individual into the core area of another is rare. Notably, several females shared home ranges, exhibiting nearly complete overlap of the home range and core area, a finding not reported previously. Because relation could influence spatial relationships, we suggest future research to quantify degree of relation among individuals before examining spatial distribution of bobcats.

***Key words:*** bobcat, core use area, DYNAMIC, home range, interaction, *Lynx rufus*, overlap.

Intersexual differences in social behavior and spacing patterns in mammals reflect differences in selection pressures and life history characteristics (Crook et al. 1976, Eisenberg 1981). Male reproductive success is closely related to finding mates, whereas female reproductive success is related to locating and effectively exploiting resources (Clutton-Brock 1989). Therefore, distribution of males across landscapes should reflect female distribution, but female distribution should be more attuned to availability of quality resources (MacDonald 1983, Sandell 1989).

Reliable estimates of home range are essential to understand a species behavioral ecology (Bekoff and Mech 1984), and areas of concentrated use within home ranges are often denoted as core areas, implying that these selected areas are of greater importance to the animal (Leuthold 1977). Previous studies have used home range overlap as a method to examine social organization within bobcat populations (Bailey 1974, Zezulak and Schwab 1980, Berg 1981). Generally, research has indicated that considerable intersexual overlap occurs with adult females frequently maintaining exclusive home ranges, and male ranges frequently overlapping other males and several females (Marshall and Jenkins 1966, Lembeck and Gould 1979, Hamilton 1982). Conversely, Zezulak and Schwab (1980) reported that female home ranges frequently overlapped, but that male home ranges were nearly exclusive in California. They suggested that strict territoriality may occur only when bobcat density is low. This contention is not supported by other literature, as exclusive intrasexual home ranges were maintained at the greatest densities reported (Lembeck and Gould 1979, Miller and Speake 1979).

Bobcats are polygynous and considered solitary carnivores, with direct social interactions between adults rare, except for males and females during breeding periods (Anderson 1987). However, no research has attempted to quantify temporal interactions among bobcats, particularly simultaneous movements of multiple individuals within shared or overlapping regions of home ranges. Therefore, our objectives were to examine season- and sex-specific home range and core area overlap, and assess temporal interactions across seasons for a population of adult bobcats in central Mississippi from 1989–97. Based on previous literature regarding spatial relationships among bobcats and bobcat ecology, we predicted that male home ranges and core areas would overlap those of females, but that adult females would maintain exclusive home ranges and core areas. Furthermore, we predicted that adult males and females would not exhibit intersexual interactions outside of breeding periods. Lastly, we predicted that access to and interactions with females were important factors influencing male spatial distributions.

## METHODS

### Study Area

This research was conducted on the 14,410-ha Tallahala Wildlife Management Area (TWMA), a 4,900 ha area owned by Georgia Pacific Corporation (GP), and surrounding private lands in sections of Jasper, Newton, Scott, and Smith counties, Mississippi. The TWMA contained 30% mature (>30 yr old) bottomland hardwood forests, 37% mature pine (loblolly, *Pinus taeda;* shortleaf, *P. echinata*) forests, 17% mixed pine-hardwood forests, and 11% in 1–15-year-old loblolly pine plantations. A tornado bisected TWMA in 1992, altering approximately 1,000 ha of mature pine and hardwood forests; most (90%) of the damaged area was replanted to loblolly pine. The GP area, located adjacent to TWMA, was managed primarily for wood fiber production with 90% of the area composed of 1–35-year-old loblolly pine plantations, and the remaining 10% in Streamside Management Zones along creek drainages. Private lands were comprised mostly of mixed pine-hardwood and short-rotation pine forests. Topography was gently to moderately rolling, with 0–20% slope. Climate was mild, with a mean annual temperature of 20°C and mean annual precipitation of 152 cm. Hereafter, the TWMA refers to both study areas and the surrounding private lands.

**Capture and Telemetry**

We captured bobcats with Number 3 and 1.5 Victor soft-catch foot-hold traps (Woodstream, Lititz, Pennsylvania, USA) from 10 January to 15 August 1989, and from 4 January to 5 March annually from 1990–1997. Captured bobcats were netted and anesthetized with Ketamine hydrochloride (Ketaset Veterinary Products, Fort Dodge Laboratories Inc., Fort Dodge, Iowa, USA) at 15 mg/kg of estimated body mass. Each bobcat was weighed, standard body measurements were taken, and each was given a unique tattoo. We separated bobcats into 3 age classes (kitten, subadult, adult) based on tooth eruption, teat condition of females, and scrotum size on males (Crowe 1975). We fitted each adult bobcat with a 175–225-g mortality-sensitive radiotransmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Subadult bobcats were not fitted with radiotransmitters because of concerns with indeterminate growth of bobcats and auspices of the Mississippi State University Institutional Animal Care and Use Committee. Drugged bobcats were placed in portable pet kennels and monitored until recovery, then released at the capture site the following morning. We conducted research under Mississippi State University Institutional Animal Care and Use Committee Protocol 93-032.

Bobcats were located by triangulation (White and Garrott 1990) using a hand-held, 3-element Yagi antenna (Wildlife Materials, Carbondale, Illinois, USA) from fixed telemetry stations ($n = 480$) ≥2 times/week. In most (92%) instances, distance from observer to bobcat was ≤1.0 km. We used 2 telemetry techniques to monitor bobcats: systematic point and sequential locations. We obtained systematic point locations by recording 2 locations weekly for each bobcat. We conducted sequential telemetry (focal runs) on a 3–6-hr basis with a location recorded on each bobcat every hour for the entire 3–6-hr period. Azimuths for a single radio location were recorded within a 15-min interval to reduce error due to bobcat movement; however, most (88%) consecutive azimuths were recorded within 6 min (4.1 ± 0.02). Triangulation angles were maintained between 45° and 135° to reduce error (Kitchings and Story 1979). Telemetry accuracy tests indicated that standard deviation from true bearing was 5.9°.

**Home Range and Core Area Overlap**

Bobcat locations were converted to a coordinate system using program TELEBASE (Wynn et al. 1990). We divided each year into breeding (1 Feb–31 May), kitten-rearing (1 Jun–30 Sep), and winter (1 Oct–31 Jan) seasons. Seasonal home range (95%) and core area (50%) contour intervals were estimated using an adaptive kernel estimator in program CALHOME (Kie et al. 1994). Area-observation curves conducted on 5 randomly chosen bobcats indicated that 30–35 locations/season were needed to estimate sizes of home ranges and core areas. Therefore, we estimated sizes of home ranges and core areas for bobcats sampled with ≥30 locations/season and monitored for ≥75% of a given season.

We used all locations (sequential and point) taken on each bobcat to estimate sizes of the home ranges and core areas. We seasonally estimated overlap of home ranges by intersecting home ranges of neighboring bobcats and determining the area of the overlap region in ARCVIEW (Environmental Systems Research Institute, Redlands, California, USA). We then superimposed point locations of each bobcat on the overlap region and counted the number of locations by bobcat within the overlap region to derive a proportion of each individual's locations within the overlap region. We assessed overlap of bobcats that shared portions of home ranges across 3 dyads (male-male, female-female, male-female combinations).

We described the spatial distribution of adult bobcat home ranges using home range overlap indices. During each season, we calculated a home range overlap index for 2 neighboring bobcats by modifying the simple ratio of Ginsberg and Young (1992) to quantify association:

$$n_1 + n_2 / N_1 + N_2 \times 100$$

Where $n_1$ and $n_2$ refer to number of locations for each bobcat within the overlap region, and $N_1$ and $N_2$ refer to the total number of locations recorded for each bobcat. We used a 2-way analysis of variance to test differences in mean home range and core area overlap indices among dyads and seasons.

**Temporal Interactions**

We used program DYNAMIC (Doncaster 1990) to assess temporal interactions among adult bobcats with overlapping or shared home ranges. Program DYNAMIC is a non-parametric procedure that probabilistically expresses the simultaneous movements of 2 individuals. The dynamic interaction test determines if 2 animals monitored simultaneously during a time interval were located within a critical distance more or less often expected if the 2 animals were moving independently (Doncaster 1990). The presence of dynamic interaction does not necessarily imply mutual awareness from the respective animals. Rather, DYNAMIC addresses whether animals are more likely to maintain a certain separation (positive interaction) or less likely (negative interaction) than expected from the configuration and use of areas within their known home ranges (Doncaster 1990). Observed separation distances between bobcats were calculated from paired x-y coordinates within a 10-min time interval. Expected differences were estimated in DYNAMIC from all possible combinations of unpaired coordinates. Observed and expected separation intervals were then estimated at 50-m intervals from 0 to 500 m. We assumed that bobcats were not likely to detect each other beyond 500 m in the forested environment of TWMA. A positive interaction occurred if observed interactions (paired) were greater than expected (unpaired) interactions. A negative interaction occurred if expected interactions (unpaired) were greater than observed (paired) interactions. Chi-square procedures were used to test significance of positive and negative dynamic interactions. All tests were performed at $\alpha = 0.05$.

## RESULTS

Male home range sizes averaged 1,769 ± 182, 1,528 ± 188, and 1,877 ± 265 ha during breeding, kitten-rearing, and winter, respectively. Male core area sizes averaged 308 ± 40, 295 ± 41, and 295 ± 40 ha during those same seasons. Female home range sizes averaged 863 ± 68, 870 ± 80, and 855 ± 136 ha during breeding, kitten-rearing, and winter, respectively. Female core areas averaged 148 ± 13, 146 ± 16, and 136 ± 14 ha during those same seasons.

### Home Range and Core Area Overlap

Interactions between dyad and season did not influence home range ($F_{4,291} = 0.61$, $P = 0.659$) or core area ($F_{4,291} = 0.46$, $P = 0.208$) overlap. Further, home range and core area overlap did not differ among seasons ($0.05 \leq F_{2,291} \leq 0.20$, $0.819 \leq P \leq 0.955$). Conversely, home range and core area overlap differed among dyads ($5.22 \leq F_{2,291} \leq 6.20$, $0.006 \leq P \leq 0.002$). Neighboring males and females exhibited greater home range overlap ($\bar{x} = 29\%$, SE = 3) than neighboring males ($\bar{x} = 18\%$, SE = 2) or females ($\bar{x} = 21\%$, SE = 4). Similarly, neighboring males and females exhibited greater core area overlap ($\bar{x} = 8\%$, SE = 1) than neighboring males ($\bar{x} = 3\%$, SE = 1) or females ($\bar{x} = 4\%$, SE = 1).

We documented 33 instances of seasonal home range overlap for neighboring males. Area of overlap averaged 431 (SE = 109), 364 (SE = 154), and 652 ha (SE = 322) during breeding, kitten-rearing, and winter, respectively. Greatest home range overlap among neighboring males occurred during breeding, but core area overlap was minimal during all seasons (Table 1).

We documented 117 instances of seasonal home range overlap among neighboring females. Area of overlap averaged 270 (SE = 47), 244 (SE = 42), and 170 ha (SE = 33) during breeding, kitten-rearing, and winter, respectively. Home range and core area overlap among neighboring females were similar during all seasons (Table 1). Additionally, several females exhibited substantial home range overlap and sharing of core areas (Fig. 1).

We documented 158 instances of intersexual home range overlap; area of overlap averaged 464 (SE = 47), 338 (SE = 44), and 384 ha (SE = 55) during breeding, kittenrearing, and winter, respectively. Home range and core area overlap were greatest during breeding periods (Table 1) and male core areas were frequently located in proximity to female core areas (Fig. 2).

### Temporal Interactions

During the breeding season, comparisons between males ($n = 3$ pairs) within 50 m were either negative or no interaction occurred, indicating that males monitored simultaneously were not located within 50 m of one another. However, most comparisons between 100 and 500 m indicated positive interactions, suggesting that males were more likely to be located within 100–500 m

Table 1. Mean (± SE) percent home range and core area overlap for adult bobcats on the Tallahala Wildlife Management Area, Georgia Pacific Corporation, and surrounding private lands, Mississippi, 1989–97.

| | | | Home range | | Core area | |
|---|---|---|---|---|---|---|
| Dyad combination | Season[a] | $n$ | % overlap | SE | % overlap | SE |
| Male | Breeding | 16 | 17 | 4 | 2 | 1 |
| | Kitten-rearing | 10 | 15 | 5 | 3 | 1 |
| | Winter | 7 | 23 | 9 | 4 | 2 |
| Female | Breeding | 49 | 21 | 3 | 4 | 1 |
| | Kitten-rearing | 48 | 23 | 3 | 4 | 1 |
| | Winter | 20 | 19 | 4 | 3 | 1 |
| Male-female | Breeding | 68 | 33 | 3 | 9 | 1 |
| | Kitten-rearing | 55 | 27 | 3 | 6 | 1 |
| | Winter | 35 | 27 | 4 | 6 | 1 |

[a]Breeding = 1 Feb–31 May, kitten-rearing = 1 Jun–30 Sep, winter = 1 Oct–31 Jan.

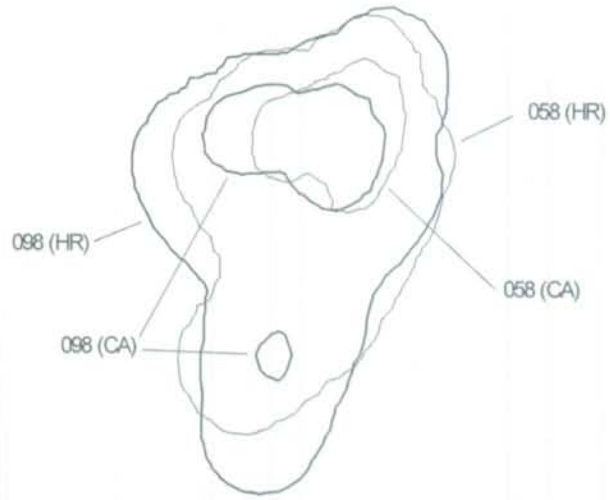


Fig. 1. Adaptive kernel 95% home range and 50% core area isopleths for 2 adult female bobcats (bobcats 058 and 098) demonstrating sharing of home ranges and core areas during the kitten-rearing season (1 Jun–30 Sep) on the Tallahala Wildlife Management Area, Georgia-Pacific Corporation, and surrounding private lands, Mississippi, 1997.

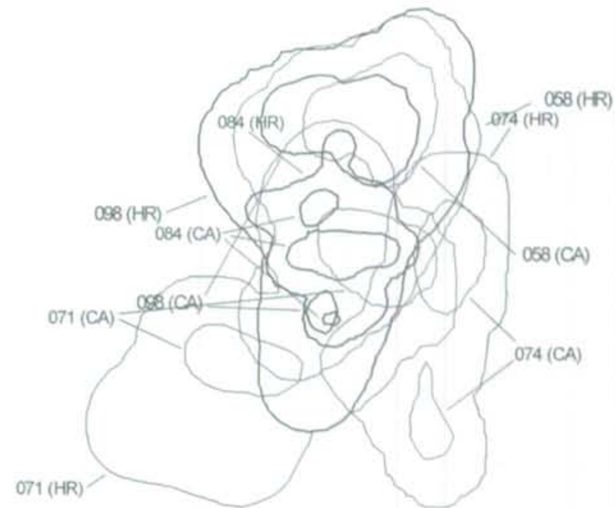


Fig. 2. Adaptive kernel 95% home range and 50% core area isopleths for 2 adult females (bobcats 074 and 084) and 1 adult male bobcat (bobcat 071) illustrating extensive home range overlap by male of female home ranges and core areas during the breeding season (1 Feb–31 May) on the Tallahala Wildlife Management Area, Georgia-Pacific Corporation, and surrounding private lands, Mississippi, 1996.

than expected. For females ($n = 16$ pairs), comparisons within 50 m indicated no interactions, but most comparisons beyond 100 m were positive, suggesting that females with overlapping home ranges and core areas were frequently located closer together than expected. For males and females ($n = 25$ pairs), several instances of presumed direct contact (separation distances <10 m) were documented and most comparisons were positive, indicating that males and females were located closer together than expected by chance.

During kitten-rearing, we noted only 1 instance of positive interactions between males ($n = 2$ pairs), whereas most interactions were negative, suggesting an avoidance among males. With 1 exception, no 2 females ($n = 15$ pairs) were located within 50 m of each other, but most comparisons from 100–500 m were positive, indicating that females were frequently located closer together than expected at these distances. Between males and females ($n = 29$ pairs), most comparisons, particularly those >100 m, indicated positive interactions. This suggests that males and females monitored simultaneously were frequently located closer than expected.

During winter, most comparisons indicated no interaction or negative interactions, suggesting that males ($n = 3$ pairs) were usually located farther apart than expected. For females ($n = 12$ pairs), most comparisons >200 m were positive; however, several females consistently exhibited negative interactions with other females, especially for those that maintained exclusive core areas. Notably, 2 females were frequently located <50 m of each other, exhibited significant positive interactions in all distance classes, and were located together on several occasions <100 m from researchers. These 2 females also shared home ranges and core areas during all seasons (Fig. 1). For males and females ($n = 20$ pairs), most comparisons >100 m were positive; however, all comparisons <100 m indicated no interaction or were negative, suggesting that males and females were more likely to be located >100 m apart.

## DISCUSSION

Most previous studies have reported that adult female bobcats frequently maintain exclusive home ranges, suggesting territoriality among females. These same studies have indicated that males frequently overlap other males and several females (Marshall and Jenkins 1966, Lembeck and Gould 1979, Hamilton 1982, Anderson 1988). Our findings do not support these studies as females on TWMA maintained overlapping home ranges in all seasons, as did neighboring males. Our finding that male-male and female-female dyads exhibited home range overlap indices around 20% during all seasons suggests a lack of pronounced intrasexual territoriality. Additionally, the near sharing of home ranges by adult females is a finding not reported in previous bobcat literature. Differences between this study and others may have resulted from larger sample size and longer duration of this study, and methods previous studies used to assess overlap (i.e., use of area of overlap only). Further, the trapping protocol used during this project may have increased the probability of capturing all bobcats within the core of the study area. During each trapping season, researchers attempted to catch all bobcats on TWMA, basing potential capture sites on the spatial distribution of home ranges for bobcats being monitored. Voids, or areas without a radiomarked female, were targeted as well as females needing collars replaced. On several occasions, females were captured in areas where researchers were attempting to recapture individuals, rather than to capture new bobcats. Therefore, we believed that most adult females within the core of TWMA were being monitored.

Females on TWMA did not exhibit pronounced territoriality at the home range level, even during kitten-rearing when females may displace conspecifics to promote kitten survival (McCord and Cardoza 1982). On average, 15% of each neighboring female's locations were within the overlap regions of adjacent females and the area of overlap was 50% as large as the average female home range during all seasons. This, coupled with the observed maintenance of nearly exclusive core areas, suggests that although females frequently tolerated overlap of used areas at outlying portions of the home range, territoriality was most prevalent at the core area level. Notably, females were often located closer together than expected, supporting contentions that females likely use areas outside the core area close to each other, but that movement of 1 female into the core area of another is rare.

Zezulak and Schwab (1980) suggested that territoriality may only occur when bobcat densities are low. Presumably, as density increased, bobcats would be less able to defend territories and would yield to neighboring adults using outlying portions of their home range. However, this contention has not been supported in other studies, as greatest bobcat densities reported (Lembeck and Gould 1979, Miller and Speake 1979) witnessed exclusive intrasexual home ranges (presumed territoriality). Densities on TWMA reported by Conner et al. (1992) were within the range of estimates reported throughout the southeastern United States and bobcat density likely increased during our study (Chamberlain 1999). Therefore, our findings suggest that territoriality at the home range level is not prevalent, but that intrasexual territoriality at the core area level is common, regardless of density.

Conner et al. (1999) reported that experience influences home range characteristics of female bobcats. Presumably, as a female gains hunting experience, she becomes more efficient and needs to hunt less. Increased hunting experience should then lead to increased success, less time spent searching for prey and wandering, and a decrease in home range size (Conner et al. 1999). Because many females were monitored for several years in our study, experience also may have influenced spatial characteristics and observed overlap among females. Females with greater experience, who are assumed to be more efficient hunters, may tolerate greater overlap from neighboring females. Experienced females with increased hunting skill and greater hunting efficiency can likely meet energetic requirements even when sharing portions of home ranges with adjacent females. Alternatively, older, experienced females likely have greater fitness relative to younger females. Experienced females may produce kittens that eventually reside adjacent to their mother, either through filling a vacancy resulting from death of another female, or potentially sharing a portion of the mothers home range. Older, experienced females may allow greater overlap of their home range if adjacent females are siblings or daughters; however, the relationship between relation and spatial overlap is unclear. Future research should examine the influence of relation among adult females on spatial characteristics across various landscapes.

Because bobcats are polygynous breeders, it is not surprising that males overlapped large portions of female home ranges and were often located closer than expected to females, particularly during breeding periods. Furthermore, our findings suggest that male core areas frequently overlap large portions of females core areas, even those core areas maintained by multiple females. This suggests that distribution of male core areas across landscapes is perhaps a function of location of female core areas and potentially, males locate and maintain core areas during breeding to optimize breeding opportunities. Because male fitness increases with increasing mating opportunities, males maintaining core areas that overlap multiple females likely increase their fitness. Additionally, males and females selected core areas dominated by 0–8-year-old pine stands, presumably because of increased prey availability and overall habitat quality (Chamberlain 1999). Therefore, males locating core areas around female core areas is likely a result of both breeding behavior and habitat requirements.

Zezulak and Schwab (1980) reported that male home ranges were nearly exclusive in California, whereas most other studies have indicated that males exhibit little territoriality at the home range level, frequently overlapping portions of other male home ranges (Marshall and Jenkins 1966, Berg 1981). Our findings indicate that males maintain overlapping home ranges, but nearly exclusive core areas, suggesting territoriality at the core area level. Besides providing quality foraging habitats, core areas also may provide sites important to bobcats, such as den sites or escape cover (Ewer 1973, McCord and Cardoza 1982). If males establish core areas to overlap multiple female core areas, males should exhibit territoriality at the core area level, particularly during breeding periods, to increase fitness. The observed lack of interactions between neighboring males during all seasons is likely a function of maintaining exclusive core areas.

## ACKNOWLEDGMENTS

We appreciate field assistance provided by R. Andrus, J. G. Burton, L. M. Conner, D. A. Edwards, K. M. Hodges, C. D. Lovell, B. W. Plowman, C. D. Spencer, and K. J. Sullivan. We appreciate substantive comments provided by L. M. Conner. Funding was provided by the

Mississippi Department of Wildlife, Fisheries, and Parks through Federal Aid in Wildlife Restoration Funds Project W-48, Study 29, the National Wild Turkey Federation, Georgia Pacific Corporation, and U.S. Forest Service. This manuscript was approved by the School of Forestry, Wildlife, and Fisheries at Louisiana State University (LSU) and the LSU Agricultural Center.

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# MULTIVARIATE HABITAT MODELS FOR BOBCATS IN SOUTHERN FORESTED LANDSCAPES

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***Abstract***: Habitat models can be useful for understanding habitat needs of a species and may serve as a tool for habitat management. Few habitat models have been developed for bobcats (*Lynx rufus*); thus we developed sex-specific habitat models for bobcats within southern managed forests using a biometric approach and geographical information system (GIS) technology. One model described female bobcat habitat as near roads, on relatively steep slopes, far from creeks, and in forested stands with small trees (i.e., early successional habitat). Jackknife and cross-validation indicated this model performed well (76 and 78.5% correct classification, respectively). Another model described male bobcat habitat as near maintenance roads and in stands with small trees. Jackknife and cross-validation indicated this model also performed well (72 and 77.5% correct classification, respectively). Prey abundance can explain importance of variables in both models. The increased number of variables retained by the female habitat model provides evidence that females are more selective than males regarding habitat use. Model validation using independent data is needed before our models are implemented.

***Key words***: bobcat, forest ecosystem, geographic information system, habitat model, *Lynx rufus*, Mississippi.

Because apex predators may regulate mesomammals (Rogers and Caro 1998, Crooks and Soule 1999, Courchamp et al. 1999) and may play a role in predator mediated coexistence of other species (Henke and Bryant 1999), management of top carnivore populations is important. Bobcats (*Lynx rufus*) represent an apex carnivore in many forested ecosystems. Published bobcat habitat models are rare (Boyle and Fendley 1987, Conner and Leopold 1998), and these models are either based on expert opinion (Boyle and Fendley 1987) or only applicable to a narrow range of habitat conditions (Conner and Leopold 1998). Previously, Conner and Leopold (1998) developed a bobcat habitat model of a national forest in central Mississippi. Although this model performed well on the national forest, it performed poorly on an adjacent industrial forest.

Habitat modeling is perhaps best viewed as an iterative process in which models are developed, tested, and refined based on test results and revised needs (Conner and Leopold 1998). Because our initial model did not perform well on an industrial forest (Conner and Leopold 1998), we do not think that models developed on an industrial forest will perform well on a national forest. However, models developed using animals from both industrial and national forests may provide a more generalized description of bobcat habitat in forested ecosystems. Therefore, we developed sex-specific bobcat habitat models using data collected on bobcats residing in a national forest (i.e., a multiple use forest management philosophy) and data collected in an intensively managed industrial forest (i.e., a timber production management philosophy) to better describe bobcat habitat within managed southern forests.

## METHODS

### Description of Study Areas

We used 2 study areas: Tallahala Wildlife Management Area (WMA, multiple use management philosophy) and forests owned and managed by Georgia Pacific (GP, timber production management philosophy) in Newton and Jasper counties in central Mississippi.

The 142-km$^2$ Tallahala WMA is located in the Bienville National Forest. Mean annual temperature was 18°C and annual precipitation averaged 152 cm. Pine (*Pinus* spp.) stands ($\geq$ 70% pine dominated with mean dbh >5.0 cm) comprised 46% of the study area. Loblolly pine (*P. taeda*) was the dominant species, whereas shortleaf pine (*P. echinata*) and longleaf pine (*P. palustris*) occurred in scattered patches. Approximately 29% of the area was in sapling stands (forested with mean dbh $\leq$5 cm). Sapling stands averaged 13 ha in size and rarely exceeded 20 ha. Bottomland hardwoods accounted for 21% of the area and were located primarily in riparian zones along major drainages. Approximately 4% of the area was in agriculture. Pines were regenerated by clear-cutting followed by site preparation and planting. Hardwood stands were regenerated using the shelterwood method or coppice management. Hardwood clear-cutting was prohibited.

The 80-km$^2$ GP study area was located adjacent to Tallahala WMA, thus weather patterns between the 2 study areas were similar. Pine stands covered 60% of the area, but 88% of pine stands on GP consisted of trees that were <33 cm dbh (as opposed to 18% on Tallahala WMA). Sapling (20%), hardwood (12%), and agriculture (8%) comprised the remainder of the study area. The land was managed primarily for timber production, and stands were regenerated by clear-cutting and planting. Sapling stands >100 ha were common. Larger clear-cuts, intensive pine management, absence of mature timber, and lack of hardwood stands on GP (relative to Tallahala WMA) permitted study of bobcat ecology under 2 different, yet common, forest management regimes.

**Geographical Information System Development**

We constructed a geographical information system (GIS) for each study area. We transferred stand boundaries from color infrared photographs to 1:24000 United States Geological Survey (USGS) quadrangles. We classified habitat into 1 of 3 types: non-forested (e.g., agriculture), pine forest, and hardwood forest. Additionally, we categorized each stand into 1 of 5 condition classes; non-forested, sapling (dbh < 5.0 cm), pole (5.1 cm < dbh < 12.7 cm), pulpwood (12.8 cm < dbh < 38.1 cm), and sawtimber (dbh > 38.2 cm). We digitized data of stands using ARC/INFO (Environmental Systems Research Institute 1992).

We also constructed coverages for roads, creeks, and elevation. We classified roads as paved, gravel, or maintenance (i.e., roads closed to the general public) and creeks as either ephemeral or permanent. We digitized road and creek coverages directly from USGS quadrangles. We obtained digital elevation models from the USGS to create elevation and slope layers. We developed 8 slope classes ranging from class 1 representing a midpoint of approximately 5.5% slope, to class 8, representing a midpoint of approximately 84.5% slope. The range of each slope class was approximately 11% (Environmental Systems Research Institute 1992). In all, our GIS contained 15 habitat variables (Table 1).

**Bobcat Capture and Monitoring**

We captured bobcats using Victor Soft-catch traps (Woodstream Corp., Lititz, Pennsylvania, USA.). Following capture, we netted and drugged bobcats with Ketamine hydrochloride (15 mg/kg body mass). We separated bobcats into 3 age classes (kitten <1.0 year; sub-adult 1–2 years; adult >2 years) based on tooth eruption, staining and wear, body size, pelage characteristics, teat condition of females, and scrotum size of males (Crowe 1975). We fitted all adult females and select adult males (i.e., males captured in interior portions of study areas) with a radiocollar (ATS, Isanti, Minnesota, USA and Wildlife Materials Incorporated, Carbondale, Illinois, USA). We monitored bobcats overnight to assess recovery prior to release at the capture site and allowed bobcats 1 week to recover from capture before we initiated radiotracking. We trapped bobcats during winters (7 Jan–15 Mar) of 1989–92. Bobcat capture and data collection followed Animal Care and Use Protocol 93-032 of Mississippi State University.

We monitored bobcats throughout the diel period using a TRX-1000S receiver and a hand-held 3-element Yagi antenna (Wildlife Materials Incorporated, Carbondale Illinois, USA). We estimated locations by triangulation from fixed points within the study areas (Cochran 1980, Kenward 1987, White and Garrott 1990). We frequently obtained ≥3 azimuths to minimize erroneous locations. To decrease error associated with bobcat movement, we allowed a maximum of 15 min between azimuths. We converted azimuths to coordinates using the program TELEBASE (Wynn et al. 1990).

Telemetry accuracy tests indicated the standard deviation from true bearings was 6° ($n = 42$). Approximately 90% of all telemetry bearings were taken <1 km from an animal. Based on our accuracy tests, a circle circumscribing the estimated location of the bobcat located 1 km from each telemetry station would cover approximately 3.5 ha.

**Model Development and Validation**

Identification of unused habitats is beneficial when developing habitat models, but it is impossible to identify unused habitats with certainty (e.g., if the site was used when the animal was not monitored; Clark et al. 1993). We attempted to reduce probability that a random point occurred at a site that was actually used by a bobcat by generating random points which did not occur within 200 m of a used location. We overlaid bobcat telemetry locations and random points onto GIS layers and determined habitat characteristics at each point.

Selection of variables for habitat modeling without prior indication of their ecological importance should be avoided (Johnson 1981; Rexstad et al. 1988, 1990; Taylor 1990). Therefore, we passed habitat variables through 3 filters before entering them into a model. The first filter eliminated non-significant ($P < 0.01$) variables using univariate hypotheses tests (i.e., $t$-test or $\chi^2$ test). A conservative alpha level ($P < 0.01$) was chosen because we feared that our large sample sizes would have sufficient power to detect statistical differences when biological differences likely did not exist.

To further reduce the variable set, we subjected remaining continuous variates to a second filter to remove correlated variables. If variables were correlated ($P < 0.05$; $|r| > 0.4$) we omitted the least significant variable from further model building efforts (Brennan et al. 1986).

We used stepwise logistic regression (LR) as the final filter and statistical tool to develop the habitat model. Type of location, bobcat or random, served as the binary response variable in modeling attempts. We calculated

Table 1. Variables used to develop bobcat habitat model on Georgia Pacific landholdings and Tallahala Wildlife Management Area in central Mississippi, 1989–92.

| Variable name | Description |
|---|---|
| TYPE | Forest type index (non-forested, pine, or hardwood) |
| COND | Stand condition (non-forested, sapling, pole, pulpwood and sawtimber) |
| EDGE | Distance[a] to edge |
| SAP | Distance to nearest sapling stand |
| PINE | Distance to nearest non-sapling pine stand |
| HWD | Distance to nearest non-sapling hardwood stand |
| RD | Distance to nearest road |
| RD1 | Distance to nearest paved road |
| RD2 | Distance to nearest gravel road |
| RD3 | Distance to nearest maintenance road |
| CRK | Distance to nearest creek |
| CRK1 | Distance to nearest primary creek |
| CRK2 | Distance to nearest ephemeral creek |
| ELEV | Elevation (class) |
| SLOPE | Slope (8 equal classes 0–90°) |

[a]All distances measured in km.

posterior probabilities (i.e., probability of bobcat use) from the final logistic regression model as a habitat suitability index (HSI, Brennan et al. 1986) for bobcats.

We subjected models to 2 levels of validation. We used jackknife validation to evaluate model predictions with data used in model construction. We also withheld approximately 20% of all locations from model building efforts. We used these locations to cross-validate model predictions as a second evaluation of the models (Capen et al. 1986, Verbyla and Litvaitis 1989).

We considered a location suitable for bobcats if the posterior probability was ≥0.5. We calculated sensitivity (i.e., bobcat location predicted correctly as a bobcat location), specificity (i.e., random location predicted correctly as a random location), and total correct classification for all validation trials. We used SAS (SAS Institute 1992) to construct and test models.

## RESULTS

We used 1,084 locations from 21 female bobcats and an equal number of random locations to develop our female bobcat HSI. Significant ($P < 0.01$) non-correlated ($P \geq 0.05$, $|r| < 0.4$) variates subjected to LR were SLOPE, RD1, RD3, CRK1, CRK2, and COND. All variables except CRK2 were retained by the stepwise procedure. The female bobcat HSI model indicated relatively steep slopes to be preferred. There was an inverse relationship between HSI and distance to primary and maintenance roads. There also was an inverse relationship between stand condition and HSI. Lastly, distance to primary creeks was related positively to HSI (Table 2). Jackknife validation indicated 76% (sensitivity = 0.82, specificity = 0.67) correct classification. The model correctly predicted 78.5% (sensitivity = 0.91, specificity = 0.66) of locations when tested using cross-validation (Fig. 1).

We used 209 locations from 9 male bobcats and an equal number of random locations to develop our male bobcat HSI. Significant ($P < 0.01$) non-correlated ($P \geq 0.05$, $|r| < 0.4$) variates subjected to LR were RD3, CRK, COND, and CLASS. Only RD3 and COND were retained by the stepwise procedure. There was an inverse relationship between HSI and distance to maintenance roads and stand condition (Table 3). Jackknife validation indicated 72% (sensitivity = 0.81, specificity = 0.63) correct classification. The model correctly predicted 77.5% (sensitivity = 0.88, specificity = 0.67) of locations when tested using cross-validation (Fig. 2).

Table 2. Logistic regression coefficients of the female bobcat habitat suitability index (HSI) model developed on Georgia Pacific landholdings and the Tallahala Wildlife Management Area in central Mississippi, 1989–92.

| Variable[a] | Coefficient | $P = 0$[b] |
|---|---|---|
| SLOPE | 0.53 | <0.001 |
| RD1 | -0.22 | <0.001 |
| RD3 | -1.33 | <0.001 |
| CRK1 | 0.30 | 0.001 |
| COND | -0.35 | 0.001 |
| Constant | 1.05 | <0.001 |

[a]SLOPE = slope class, RD1 = distance to paved road, RD3 = distance to maintenance road, CRK1 = distance to primary creek, COND = stand condition class.
[b]Probability that coefficient = 0 using a $\chi^2$ test statistic.

## DISCUSSION

Johnson (1981) stated 20 observations plus 5 observations for each independent variable should be used as a rule of thumb in establishing minimum sample sizes for multivariate analyses. Using this recommendation, sample sizes associated with our models should have been

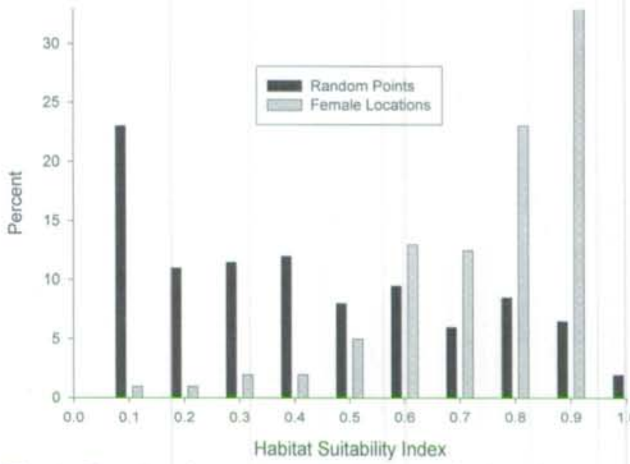


Fig. 1. Results of a cross-validation test of a female bobcat habitat suitability index (HSI) model developed on Georgia Pacific landholdings and the Tallahala Wildlife Management Area in central Mississippi, 1989–92. Shown is percentage of bobcat and random locations relative to habitat suitability index.

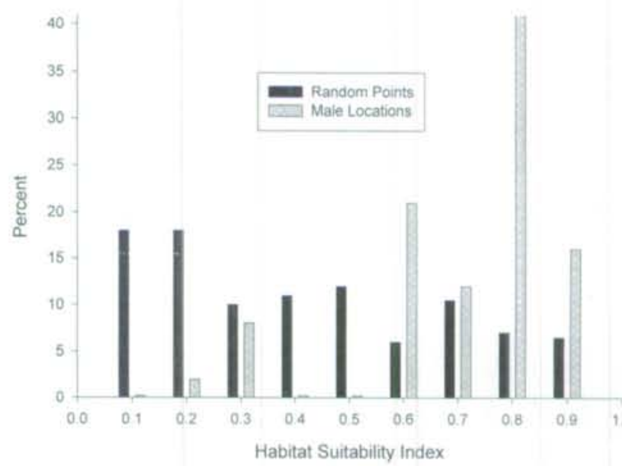


Fig. 2. Results of a cross-validation test of a male bobcat habitat suitability index (HSI) model developed on Georgia Pacific landholdings and the Tallahala Wildlife Management Area in central Mississippi, 1989–92. Shown is percentage of bobcat and random locations relative to habitat suitability index.

Table 3. Logistic regression coefficients of the male bobcat habitat suitability index (HSI) model developed on Georgia Pacific landholdings and the Tallahala Wildlife Management Area in central Mississippi, 1989–92.

| Variable[a] | Coefficient | $P = 0$[b] |
|---|---|---|
| RD3 | -1.16 | <0.001 |
| COND | -0.30 | 0.001 |
| Constant | 2.24 | <0.001 |

[a]RD3 = distance to maintenance road, COND = stand condition class.

[b]Probability that coefficient = 0 using a $\chi^2$ test statistic.

adequate because the least observation:variable ratio was approximately 100:1.

In general, random locations were predicted with less accuracy than were used locations. Habitat models that are based on used and random locations are expected to misclassify some random locations as suitable locations because some random locations used in model development were likely suitable habitat (Clark et al. 1993).

Bobcats are predators of small- to medium-sized mammals, reptiles, and birds (Fritts and Sealander 1978, Anderson 1987). Similarly, small mammals and rabbits occurred most frequently in bobcat diets on TWMA and GP (Chamberlain and Leopold 1999). On our study areas, these prey were most abundant in early successional habitats (Conner 1991); thus bobcat use of areas near and within sapling stands was likely because of prey abundance in these areas (Conner et al. 1992, Conner and Leopold 1993). Bobcats use seldom-traveled roads as travel corridors and for hunting (McCord 1974, Hall and Newsome 1976). This can explain distance to roads as a discriminator in both male and female habitat models. Notably, RDS1 was not a predictor in the male habitat model. Primary roads were located on study area peripheries, and we only monitored male bobcats that were captured at study area interiors. Therefore, lack of importance of RDS1 in the male model was likely a result of our monitoring protocol rather than a result of bobcat behavior.

Most pine stands in central Mississippi are located in upland sites and are harvested on a relatively short rotation. Thus, importance of slope to female bobcats may be an artifact of the presence of early successional habitats and the prey associated with these habitats in upland sites. However, bobcats may select more rugged terrain independent of forest type and condition (Zezulak and Schwab 1979, Hamilton 1982).

The female bobcat habitat model indicated that distance to creeks was related positively to HSI. However, there is no ecological reason for female bobcats to avoid creeks. Indeed, Yoakum (1964) observed bobcats fishing in a shallow portion of a river. We believe that the apparent avoidance of creeks by female bobcats resulted from a lack of early successional habitat near creeks, with this lack of early successional habitat being a result of forest management guidelines.

Male bobcats are habitat generalists relative to females (Bailey 1981, Sandell 1989, Conner et al. 1992). We retained 4 predictive variables in our female bobcat habitat model and only 2 variables in our male bobcat habitat model. Although sample sizes used in developing models differed between the sexes, we believe that the increased number of variables retained in the female model is, at least partially, the result of more specific habitat preferences of female bobcats.

Cross-validation and jackknife procedures yielded similar results and indicated models performed better than random. Because no independent data were available for testing the models, the applicability of these models to other forested areas within the Southeast is uncertain. Intuitively, these models should perform better than within-area models because they were developed using a much more diverse data set. Further testing is necessary on independent data sets before extrapolation of the models to other areas.

## MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Bobcats are important as an apex carnivore, but it is doubtful that wildlife managers will ever establish a habitat management plan with the goal of improving bobcat habitat. Fortunately, our models indicate that bobcats are associated with habitat traits that are promoted and maintained as a by-product of current forest management practices.

Bobcat habitat is perhaps best defined by prey abundance (Anderson 1987). Within southern ecosystems, prey abundance is often greatest within early successional habitats. Therefore, forest management practices that maintain early successional habitat should benefit bobcats.

Early successional habitat can be created and maintained using even- or uneven-aged forest management. However, our models of bobcat habitat were developed on areas using an even-aged approach to forest management, and these models would likely perform poorly if used within an uneven-aged forest management system. Because high prey abundance can be achieved within an uneven-aged forest management system, bobcat-habitat relationships within uneven-aged forested systems warrant investigation.

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# UTILITY OF BOBCAT OBSERVATION REPORTS FOR DOCUMENTING PRESENCE OF BOBCATS

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***Abstract*:** New York has had regulated hunting and trapping seasons for bobcat *(Lynx rufus)* in approximately 33% of the state since 1976. To assess bobcat distribution in other parts of New York, we solicited observations of this species throughout the state for a 3-year period beginning in 1995. The observations document bobcat presence in towns scattered across New York except Long Island. Frequency of observations was greatest for towns with records of bobcat harvest, suggesting that bobcat densities were lower outside harvested areas. By comparing the incidence of observation reports with bobcat harvest data, we infer that the use of our observational data provides a conservative approach to document presence of this species.

***Key words*:** bobcat, distribution, *Lynx rufus*, New York, population status, range, sightings.

Bobcats are present in much of North America (Wilson and Ruff 1999), but reportedly absent from an area in the northcentral United States including western New York, western Pennsylvania, Ohio, Indiana, and parts of Tennessee, Michigan, Illinois, Wisconsin, Iowa, Missouri, and South Dakota (Deems and Pursley 1978). According to DeKay (1842), the bobcat was common at the time of European settlement in what is now New York, including Long Island, but was extirpated from some parts of the state by the mid-19th century.

Prior to 1976, the bobcat was unprotected in New York and could be killed at any time and by any method. Bobcats also were subject to bounties in several counties until 1971. In 1976, state law provided protection by classifying the bobcat as a small game species. Regulated hunting and trapping seasons were established the following year in those areas where bobcat populations could support harvest. Central and western New York were closed to harvest at that time. Seasons have continued with minor modifications in areas and dates until the present (Fig. 1). Several references indicate that bobcats are absent from the St. Lawrence valley and western New York (Deems and Pursley 1978, McCord and Cardoza 1982, Wilson and Ruff 1999); however harvest records confirm their presence in much of the St. Lawrence valley.

In those parts of New York occupied by bobcats, population density varies but is low compared to values ranging from 0.04–2.74/km$^2$ reported for other parts of the United States (McCord and Cardoza 1982). Late-winter densities in New York during 1977–81 ranged from 0.02/km$^2$ in the central Adirondacks to 0.06/km$^2$ in the western Catskills (Fox 1990). Consistent with the low density in the central Adirondacks, exceptionally large home ranges and indications of marginal climate and habitat conditions for this species were found.

The secretive nature of bobcats and their low densities in many areas means that they are observed infrequently relative to many other carnivores. Because of this, harvest assumes a key role in documenting occupied bobcat range. In areas that are closed to harvest, observations and road kills are typically used to document their presence. However, prior to 1995, few bobcat observations were reported from parts of New York closed to harvest. We assumed these few observations were of immigrants from other states or from parts of New York known to be populated by bobcats. Nevertheless, farmland abandonment and vegetative succession in these areas had created habitat conditions similar to those in areas already occupied by bobcats. We estimated that there could be up to 17,000 km$^2$ of suitable but poorly occupied habitat in the state and developed this study to improve our understanding of statewide bobcat distribution.

## METHODS

Beginning in 1995, we solicited reports of bobcat observations from several types of outdoor recreationists using department publications, postcards to individual trappers and houndsmen, and letters to birding groups and licensed hunting guides. We also obtained bobcat sightings from archery deer hunters in several parts of the state. Reports from all sources were reviewed for completeness and credibility. To qualify as complete, reports needed the name of an observer, a date including year, and a location identifiable as a valid town within the state. We excluded reports based on bobcat vocalizations, tracks (except those from trappers or houndsmen), and all secondhand reports for which we could not contact the


Fig. 1. Areas of New York open to bobcat harvest by hunting and trapping during 1998 (shaded). Labels indicate place names mentioned in the text.

original observer. Observations by trappers and houndsmen and the majority of records from areas already known to be occupied by bobcats were assumed accurate. For observations from other sources and outside known bobcat range, we attempted to interview observers by telephone or mail about the circumstances of the observation. Based on the follow-up interviews we excluded records with doubtful species identification from files used for mapping. However, to prevent bias due to nonrandom selection of reports for follow-up, all complete records, incuding those with doubtful species identifications, were retained for analysis in this report.

Observations ranging from 1994 to 1999 were summarized by town according to a list of 944 jurisdictions in New York. We used the criteria of observations during all 3 years of the study to confirm a town as bobcat range. Towns with observations in 2 years were considered probable bobcat range, and towns with bobcat observation reports in only one year were considered possible bobcat range.

Bobcat harvest was tabulated by means of a regulation that requires all hunters and trappers who harvest a bobcat to submit the untanned pelt or carcass to department personnel to be affixed with a locking plastic tag. Location and date of harvest were recorded at this time.

We tabulated the number of years with ≥1 observation report(s) for towns in 3 groups as follows: (1) towns with harvest of ≥1 bobcat(s) over the duration of this study (H+), (2) towns open to bobcat harvest with no harvest occurring over the duration of this study (H-), and (3) towns closed to harvest (C). We calculated 2-way chi-square tests of observation reports vs. harvest and confirmation vs. harvest, respectively, combining H- and C groups to perform these tests. To investigate the likelihood of confirming occupied bobcat range by observation reports, we assessed whether observation reports would have confirmed bobcat occupation in each of the 247 (H+) towns during the period from the 1994–95 through the 1998–99 harvest seasons.

## RESULTS

We received 938 complete reports of bobcat observations that occurred between 1994 and early 1999. Observations occurred in 394 towns scattered throughout New York except Long Island (Fig. 2). This represents 42% of the jurisdictions on our list and 51% of the land area. More than half of the towns with observations ($n = 213$) were in the H- or C group; however, occurrence of observation reports for a town was related to occurrence of harvest ($X^2 = 136.8$, $P < 0.0001$). The association with harvest also was strong

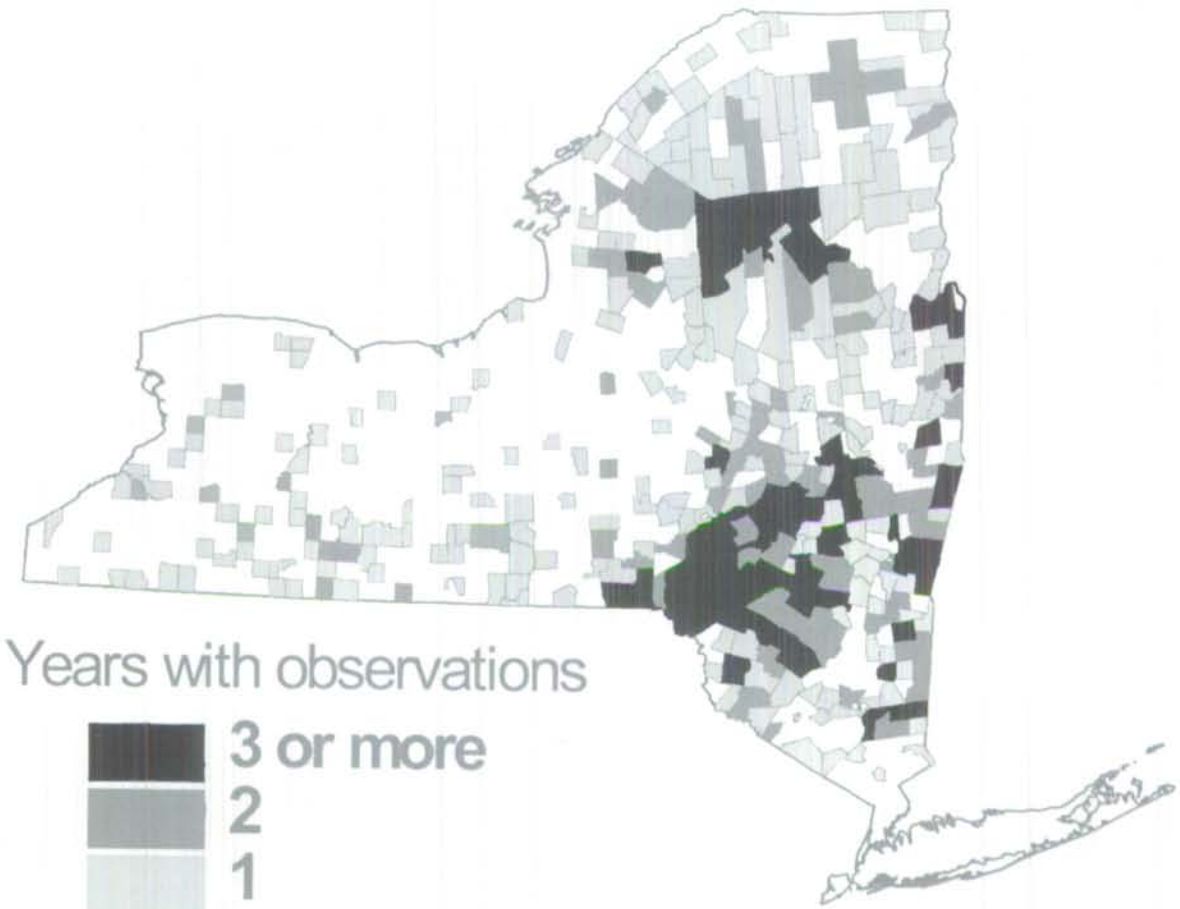


Fig. 2. Towns with bobcat observation reports in New York, 1994–99. Reports with doubtful species identifications were excluded.

for towns with observation reports in ≥3 years ($X^2$ = 55.3, $P < 0.0001$).

Of the 247 towns with bobcats harvested over the duration of the study (Fig. 3), 73.2% had ≥1 bobcat observation reports. However, only 19.4% of these towns would have been confirmed as occupied by bobcats using the criterion of ≥3 years with observation reports. An additional 20.2% would have been classified as probable occupied range, and another 33.6% as possible range.

During 1996–97, we calculated numbers of observation reports relative to hunting license sales within 3 portions of the state (Table 1). Results indicated a higher proportion of observations in the southeast section of the state than the northern or western portions.

Table 1. Observation reports vs. hunting license sales (big game and sportsmen licenses) for 3 areas of New York, 1996–97.

| Area | Observations | Sales | Observations/$10^4$ licenses |
|---|---|---|---|
| North | 49 | 85,738 | 5.72 |
| Southeast | 134 | 129,773 | 10.33 |
| West | 54 | 301,648 | 1.79 |

## DISCUSSION

Observation reports are commonly used to document presence of bobcats in areas not open to harvest (Woolf and Nielsen 1999). We found that soliciting reports through the state hunting and trapping regulations guide was highly effective, with roughly half of reports being stimulated by this means.

For consistency with harvest information, we used town or city as reporting entities to tabulate observations. Other landscape units, including counties, are often used to document presence of vertebrate species. Choice of a reporting entity affects precision of subsequent analysis. Under equivalent conditions, larger areas are more likely to produce an occurrence within their boundaries than are smaller areas. Jurisdictions in our list of towns varied in area from 2.8–1,294 km². This variation in size contributed to the frequency of observation reports in a town. Towns having observation reports or harvest reports were larger than average ($\bar{x}$ = 169.1 km² for towns with observation reports, 209.7 km² for harvested towns, and 138.9 km² for all towns on our list).

Although we used harvest as a standard for documenting areas occupied by bobcats, several factors affect the likelihood of harvest in towns where

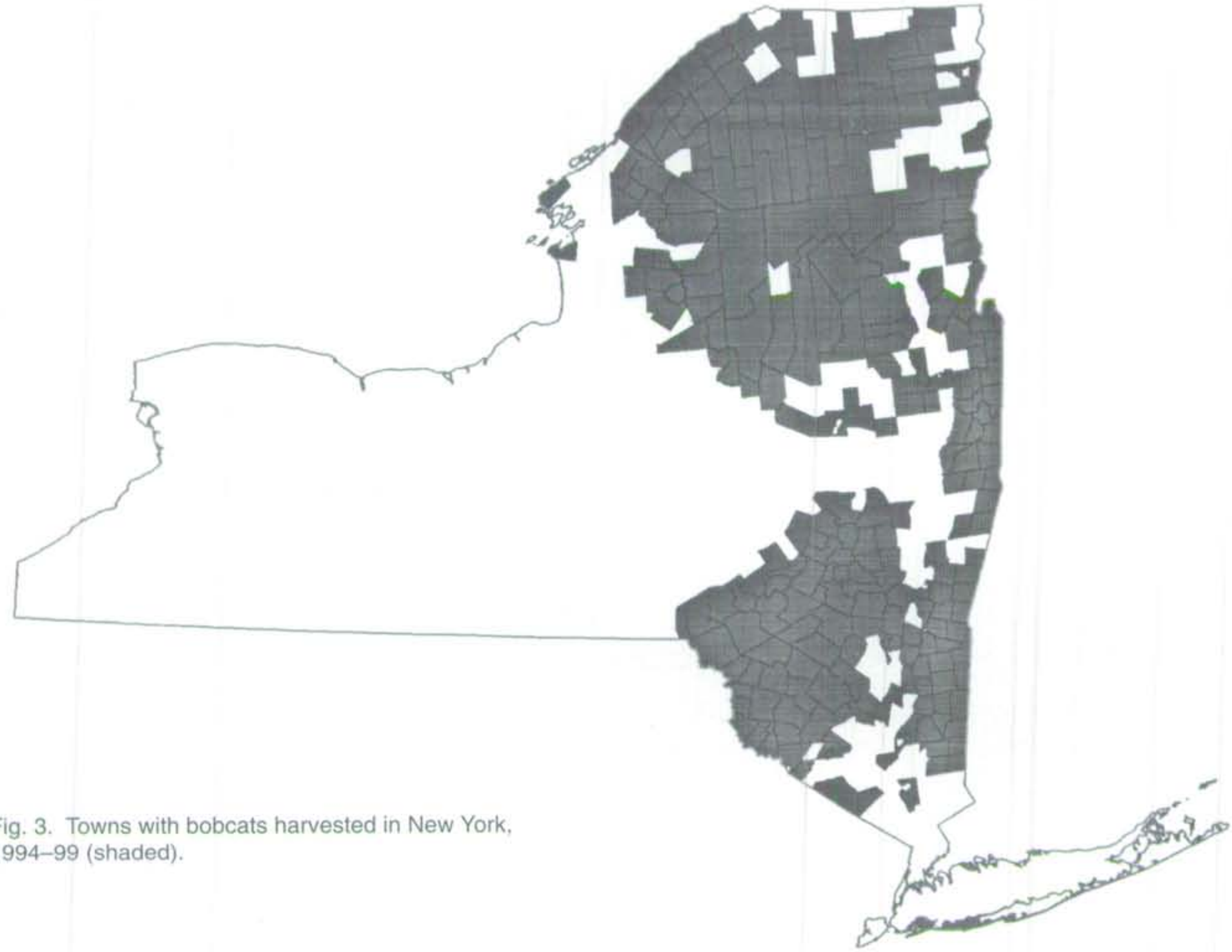

Fig. 3. Towns with bobcats harvested in New York, 1994–99 (shaded).

bobcats occur and bobcat harvest seasons are held. As with observation reports, town size influences the likelihood of harvest in that town. Other influences include length and timing of the harvest season, amount of land area open to bobcat harvest, and number and distribution patterns of potential bobcat harvesters.

Hunting and trapping seasons for bobcat are set on the basis of 85 Wildlife Management Units (WMUs). For the WMUs open to bobcat harvest, season length in a typical year varied from 37 to 149 days. Season timing is more significant than season length however, because much of the bobcat harvest occurs during the deer hunting season when large numbers of hunters are afield. Bobcat seasons in all WMUs open for bobcat harvesting currently overlap with deer hunting seasons. Because deer hunters are dispersed throughout all parts of the state except metropolitan areas, harvest data can be used to represent bobcat occurrence for areas where bobcat seasons are open.

A greater problem arises on the margins of the open areas. Since WMU boundaries rarely conform to town boundaries, many towns are split between $\geq 2$ WMUs. Along the edge of the area open for bobcat harvest, towns are commonly split so that only part of the town is open to bobcat harvest. For our analysis, towns partly open were considered open to harvest. Some of these towns had <10% of the land area included in the open area. This accounts for several towns which had no harvest over the period of the study but did have observation reports.

While a single record of harvest could confirm a town as occupied bobcat range, our criterion for observations required 3 years with an observation report to confirm a town as occupied by bobcats. Where bobcat range is expanding, our criterion of continuity over time provides some protection from mistaken town confirmations due to errors in species identification or observations of transient individuals. While the possibility of transient animals or location errors exists even for harvested bobcats, species identification by department staff with a carcass or pelt in hand eliminates a large source of the uncertainty in documenting resident populations.

Comparison of the observation and harvest maps (Figs. 2 and 3) suggests the limitations and strengths of observation data and the town classification criterion. Observation reports, screened for reliability, provide a source of data that is independent of bobcat harvest and covers a broader geographic area in New York. Despite this, we found much overlap between towns confirmed by multiple years of observations and delineation of occupied range based on harvest. While towns across the state were classified as possible or probable bobcat range based on 1 or 2 years of observations, those towns that qualified as confirmed by observations were clustered near areas where harvest occurred. Of the 64 towns classed as confirmed by observations, all but 4 overlapped or were adjacent to towns where harvest occurred.

We examined or controlled for the influence of 3 factors potentially contributing to the association of observation reports and harvest. These factors included the possibility of redundant observation and harvest reports for a single animal, the increased level of scrutiny given to reports from outside known bobcat range, and a possible higher density of observers within areas open to harvest. To examine the influence of redundancy in our methodology, we searched for redundant reports in the observation and harvest databases. Less than 1% of all observation reports appeared to refer to a harvested animal, based on criteria of similar dates and locations and names of the person reporting. To eliminate bias due to scrutiny of observation reports in non-traditional areas, we used all complete observation reports for calculation, including the 7% overall ($n = 67$) that were evaluated by follow-up interview as dubious species identifications.

Both human population density and hunter density contributed to observer density and varied widely throughout New York. The majority of our observers were hunters, suggesting that an index of hunter density would be useful in interpreting the relative number of observation reports from different areas. When we related numbers of observation reports to hunting license sales within 3 large areas of the state, results ranked consistently with our preconceived notion of relative bobcat abundance based on the most recent density estimates available for eastern New York. For the northern, central, and western areas of the state, incidence of observations over this period was roughly equivalent, but potential observers based on license sales varied threefold. We conclude that low bobcat density is the most likely explanation for the relatively low number of observation reports from most areas outside traditional bobcat range in New York.

## MANAGEMENT IMPLICATIONS

This study provides evidence of bobcat occurrence throughout central and western New York and the Mohawk River valley with a consistency too great to be attributed to immigration. However, the relative rarity of observations in these areas, along with relatively high density of potential observers, suggests that bobcat population densities are lower than in traditionally occupied areas of eastern New York.

Systematic collection and evaluation of observation reports is valuable in documenting bobcat distribution, especially in areas where bobcat harvest seasons are not established. Active solicitation of observation reports is a relatively economic means of documenting presence of this species. Three years of solicitation from outdoor recreationists resulted in observation reports in about 75% of the 247 towns where harvest occurred. Our more conservative occupation criterion, requiring 3 years of observation reports to confirm a town as occupied range, classified <20% of towns with harvest as occupied range. Jurisdictions which depend on observation reports from the public to document occurrence of relatively uncommon species will benefit from the considerations in this report.

## ACKNOWLEDGMENTS

The authors are grateful for assistance from Mark Brown, Robert Gotie, Scott Smith, and Gaye Somogie, all of the New York State Department of Environmental Conservation, and from the many individuals who contributed sighting reports. This work is a contribution of Federal Aid in Wildlife Restoration Project W-173-G.

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# EVOLUTION OF WISCONSIN'S BOBCAT HARVEST MANAGEMENT PROGRAM

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***Abstract:*** Wisconsin's bobcat (*Lynx rufus*) harvest management program has changed dramatically during the past 4 decades. The state paid bounties on bobcats until 1964 and some counties continued bounty payments for several years thereafter. In 1970, the bobcat harvest season was reduced from all year to 5.5 months. Since then, harvest regulations became increasingly restrictive. Currently, Wisconsin's bobcat harvest season is only 2.5 months long and restricted to the northern third of the state. A limited number of harvest permits are issued each year to hunters and trappers selected through a preference lottery system. Concomitant with the increased restrictions on harvest has been increased agency and public concern about the status of the species and increased research and surveys on bobcat population dynamics, including mandatory harvest registration, carcass analyses, harvester and agency questionnaires, snow-track surveys, and population modeling. Wisconsin's management program was challenged in 1990 when the Coalition for Bobcat Preservation petitioned the state to list the bobcat as a threatened species. We summarize the Wisconsin Department of Natural Resources' (WDNR's) response to this petition and the subsequent legal proceedings that culminated in the Wisconsin Supreme Court affirming the agency's decision not to list the bobcat as a threatened species. In addition, we will review the available scientific information upon which the agency's harvest management decisions are based.

***Key words:*** animal rights, bobcat, harvest, lawsuit, *Lynx rufus*, management, monitoring, population, threatened species, Wisconsin.

Changes in societal attitudes toward predators during the past 40 years have been reflected in dramatic changes in the management of bobcat harvests in Wisconsin. We describe the changes in the Wisconsin Department of Natural Resource's (WDNR's) population monitoring program and harvest management strategies during this period. Despite increasing knowledge about bobcat population status and increasingly restrictive harvest regulations, Wisconsin's management program was challenged in 1990 when the state was petitioned to list the bobcat as a threatened species. We summarize the WDNR's response to this petition and the subsequent legal proceedings. In addition, we review the available scientific information upon which the agency's harvest management decisions are currently based.

## BOUNTY YEARS

Bobcats were apparently distributed throughout Wisconsin at the time of European settlement in the mid-1800s (Jackson 1961). The first attempt to manage bobcat harvest in Wisconsin was in 1867 when a $10.00/animal bounty was offered by the state (Keener 1971). Bounty payments were reduced to $5.00 in 1923. During the next 40 years the number of bobcats bountied each year fluctuated widely from <50 to over 1,000 (Fig. 1). The average number of bobcats bountied per year during this period was 425. The distribution of bobcats in Wisconsin was largely reduced to the northern third of the state by the mid-1900s. The state discontinued bounty payments in 1964, but some counties continued them until 1970.

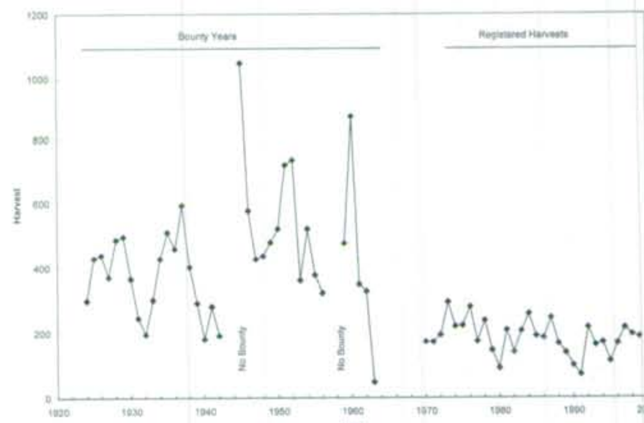


Fig. 1. Estimated number of bobcats harvested in Wisconsin, 1923–99. Estimates prior to 1964 were based on bounty payments, those after 1973 on mandatory harvest registration.

## ERA OF INCREASING PROTECTION

Although the state no longer paid bounties after 1963, bobcats were still unprotected and year-round hunting or trapping was allowed until 1970. Because of increasing WDNR and public concerns about their status in Wisconsin, in 1970 the harvesting of bobcats was restricted to a 5.5-month open season (mid-Sep–Feb). There was no daily or seasonal bag limit. In 1972 the season was reduced to 4.5 months.

In 1973, the Endangered Species Committee of the WDNR considered the status of bobcats to be questionable (Creed and Ashbrenner 1976). That year registration (inspection and tagging by WDNR staff) of all harvested bobcats was mandated. In addition, research on distribution, relative abundance, and habitat associations of bobcats was initiated. Beginning in 1976, experimental winter track count surveys were conducted in 3 counties to assess the potential of this survey technique for monitoring bobcat population trends (Klepinger et al. 1979). The hunting and trapping season was further restricted to 3 months in 1978. Winter track surveys were expanded to 17 northern counties in 1977.

Since 1980, harvesting of bobcats has been restricted to the portion of the state north of state highway 64, approximately the northern one-third of the state (Creed and Ashbrenner 1983). In addition, the open season was reduced to 2 months, a seasonal bag limit of 1 was established, and hunters and trappers were required to apply for a permit prior to the season. However, there was no limit on the number of harvesters who could receive a permit. In 1983, the season was lengthened to 2.33 months to make the opening concurrent with the general trapping season in northern Wisconsin. During the 1970s and early 1980s, harvests of bobcats averaged 201 but fluctuated between 90 and 296 (Fig. 1). Creed and Ashbrenner (1983) recommended that annual bobcat harvests be limited to ≤200.

Also in 1983, the WDNR began requiring that bobcat hunters and trappers surrender the carcass of harvested bobcats for determination of age, sex, and reproductive history. Information from collected carcasses was combined with information on size of harvest in a population model. The model was originally developed by the Minnesota DNR and was patterned after the POP-II big game population model (Bartholow 1986).

During 1985–87, scent-station transects were evaluated as a potential index to bobcat population trends. Bobcat visitation rates were fairly low and it was concluded that the survey lacked the power to detect bobcat population changes of moderate size with a reasonable amount of effort. Consequently, scent-station transects were discontinued.

## MANAGEMENT SYSTEM CHALLENGED

In March 1990, the Coalition for Bobcat Preservation petitioned the WDNR to list the bobcat as a state-threatened species. The petitioners noted that the number of bobcat harvest permits issued increased from 1,840 in 1980 to >5,000 in the late 1980s, while the number of bobcats harvested/1,000 permits declined from an average of 56 bobcats/1,000 permits in 1980-87 to 30 bobcats/1,000 permits in 1988 and 26 bobcats/1,000 permits in 1989 (Fig. 2). They concluded from these data that the population was in jeopardy. They argued that in light of uncertainty about the size of the population it would be prudent to "err on the side of caution" and stop legalized killing. They further argued that killing bobcats deprived non-consumptive users the opportunity to observe bobcats in the wild, and that trapping and hunting bobcats were unethical and irresponsible activities and were in conflict with positive, progressive wildlife ethics.

In response to the petition, the WDNR conducted an environmental analysis of scientific evidence presented in the petition and all other information available about the status of bobcats in Wisconsin in accordance with Wisconsin Environmental Protection Act processes. As part of the analysis, the WDNR requested that Lloyd B. Keith and Stanley A. Temple, professors in the Department of Wildlife Ecology at the University of Wisconsin, and William E. Berg, a furbearer research biologist for the State of Minnesota, review the available information and comment about Wisconsin's management system and the proposal to list bobcats as a threatened species. Information reviewed included harvests during 1973–89, age and sex-structure of harvest, pregnancy rates and litter size, winter track counts, scent-station surveys, and the population model.

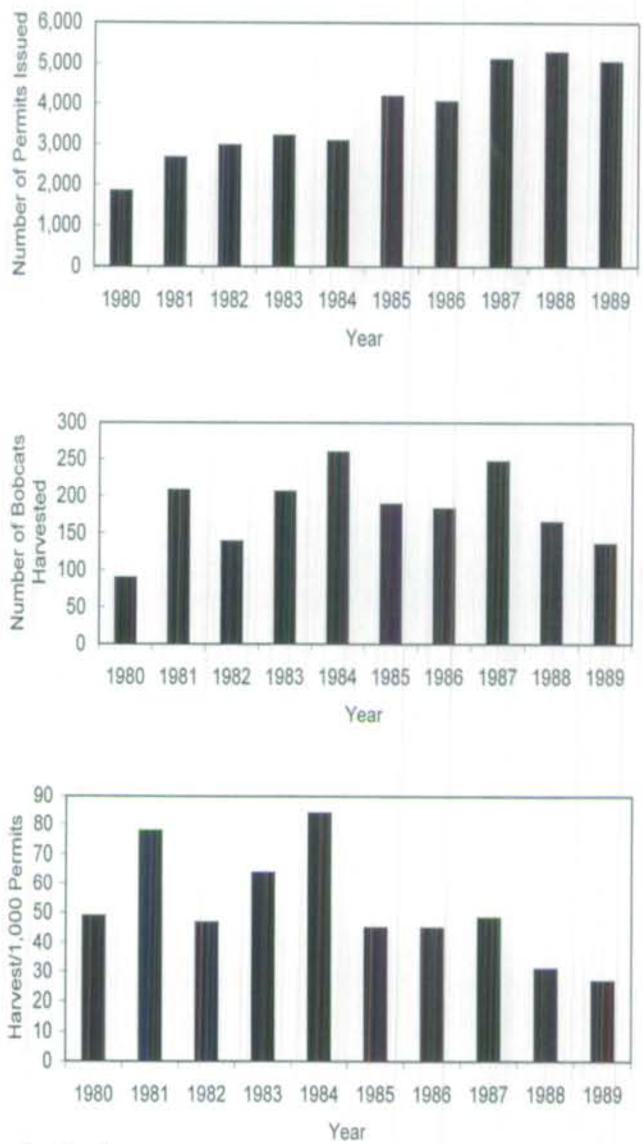


Fig. 2. Harvest success analysis used by the Coalition for Bobcat Preservation as the basis for their petition to list the bobcat as a threatened species.

Both university professors concluded that available information did not support the claim of the petitioners that the bobcat population was threatened. However, they also stated there was insufficient evidence to conclude that the population was stable. They felt none of the available indices of bobcat population trends were capable of detecting changes in the population with current levels of sampling. They both expressed concern about an increasing percentage of kittens in the harvest during the mid-1980s, suggesting one possible reason for this could be overharvest of adults. Both professors attempted to calculate estimates of population size from the available data. The resulting estimates varied considerably with several estimates considerably lower than the WDNR's estimate that was based on simulations using the Minnesota population model. In contrast, the Minnesota furbearer biologist concluded that the available data indicated to him that the population was close to stable but he recommended that Wisconsin intensify its population surveys.

Based on reviews by these independent experts, and its own analyses, the WDNR's Environmental Analysis concluded in 1991 that it was not necessary to list the bobcat as a threatened species. This conclusion was based on surveys that suggested relative population stability (winter track counts, observations of live bobcats by WDNR field personnel, reported numbers of bobcats run/day by hunters using dogs, and age and reproductive data from carcasses of harvested bobcats). The WDNR questioned whether the decline in harvest per permit issued during the 1980s (the basis of the petitioners' claim of a declining population) accurately reflected population trends, because harvest permits were free during this period and many people obtaining permits may not have actively pursued bobcats. The WDNR believed that any population decline could be offset with modification of harvest and recommended the development of a quota system to limit the number of harvest permits issued. The department informed the petitioners of its decision to not list the bobcat as a threatened species. A new harvest permit quota system was approved by the legislature and implemented in 1992.

The original petitioners joined with The Fund for Animals and petitioned the Dane County Circuit Court for a Review of an Administrative Decision. Wisconsin statutes permit a court to set aside or modify an agency's action if the agency has erroneously interpreted a provision of law or if the factual finding is not supported by substantial evidence. The petitioners claimed that the WDNR's decision to not list the bobcat as a threatened species was contrary to the intent of the Wisconsin Endangered Species Act (WESA) and the decision was not supported by substantial evidence. They cited the university professors' conclusions that the available evidence was inconclusive regarding population trend and the scientific uncertainty over population estimates and claimed that the legislative intent behind the WESA was to err on the side of protecting a species if there was uncertainty regarding its fate. Further, they argued that the WDNR's decision should be reversed because there was no scientific evidence to support the agency's conclusion that the bobcat was not threatened.

The Circuit Court's ruling in September 1992 affirmed the WDNR's decision not to list the bobcat as a threatened species. The court concluded that the petitioner's claim that the WDNR's decision was not supported by substantial evidence was groundless. The court found that the agency's decision was made after soliciting the opinion of a variety of scientific experts and a careful review of data on harvest, reproductive rates, and age- and sex-structure of the population. The court acknowledged that different interpretations of the data were possible, but believed there was substantial evidence to support the WDNR's decision. The Circuit Court concluded that lack of information was not a basis for listing a species as threatened.

The petitioners appealed the Circuit Court's decision to the Wisconsin Court of Appeals. In July 1993, the Court of Appeals concluded that the WDNR's interpretation of the WESA was reasonable and its decision in this matter was entitled to great deference because the agency had substantial experience in protecting threatened and endangered species, employed persons with the requisite technical competence and specialized knowledge in wildlife management, and had specialized knowledge related to the bobcat population in Wisconsin. The court found that the legislative intent of the WESA was to delegate listing decisions to the WDNR, and therefore the WDNR's interpretation of the statue was entitled to deference. Wisconsin statute requires the court to give due weight to agency decisions and to uphold them if they are reasonable, even if an alternative view is also reasonable. The appeals court concluded that the burden was upon the petitioners to establish that the agency's decision was not credible; the WDNR was not required to show the credibility of its decision. Finally, the appeals court concluded that the implementation of the quota harvest system accounted for many of the petitioners' concerns, as well as ensuring that the WDNR would continue to be able to make decisions based on the best available scientific data.

The petitioners then appealed to the Wisconsin Supreme Court. In June 1994, the Supreme Court affirmed the WDNR's decision. The Supreme Court concluded from the language of the WESA that the legislature intended for the WDNR to use its sound discretion in making species listing decisions and that the agency's decision was not outside the range of discretion delegated to it or an erroneous exercise of discretion. The court stressed that the WESA mandated that listing decisions are to be based on scientific data. The court found that the available scientific evidence on the status of Wisconsin's bobcat population was inconclusive; it did not support the petition's claim that bobcats were threatened, nor did it demonstrate that the bobcat population was healthy. The court rejected the petitioner's interpretation of the WESA that the state should err on the side of protection in the face of scientific uncertainty. The court stated that the WDNR had an implicit responsibility to monitor potentially declining animal populations so that scientific evidence would be available and concluded there was no indication in this case that the WDNR abdicated this responsibility.

## SCIENTIFIC BASIS FOR HARVEST MANAGEMENT

The legal challenge to Wisconsin's bobcat harvest management was one stimulus that contributed to a recent evaluation by the WDNR of the scientific basis for management decisions. Key questions in the analysis were whether the level of scientific knowledge was reasonable for the agency's management responsibilities and whether the scientific knowledge should be bolstered to make better decisions. The resulting report included a conceptual framework for the evaluation of the information needed to manage a harvested wildlife species (Wisconsin Department of Natural Resources 1995). This framework recommended indices of harvest and population change and user statistics for all harvested species. Additional information needs were identified if the species was a habitat specialist; was limited by environmental extremes, diseases, or contaminants; or had a low reproductive potential and was vulnerable to harvest. When this framework was used to evaluate bobcats, the following information needs were identified: mandatory harvest registration, population index, population model, user statistics, market value survey, and periodic habitat inventory.

The WDNR has required mandatory registration of harvested bobcats since 1973. Registration has provided timely information on the size, date, location, and method of harvest. Currently, harvesters are required to register bobcats ≤5 days after the close of the season. Beginning in 2001, successful hunters and trappers must register their animal ≤5 days after the month of harvest. The WDNR has emergency authority to close the season early if in-season registrations indicate that harvests are likely to exceed the harvest quota.

WDNR primarily relies on winter track surveys as an index to bobcat population changes. Track surveys have been conducted annually across northern Wisconsin since 1977 (Fig. 3). However, bobcat encounter rates are relatively low and during the 1980s varied considerably from year to year. As a consequence, the power of the survey to detect moderate levels of population change is relatively low. Interestingly, it appears that during the 1990s, annual variability has been lower and an increasing trend in track encounters is suggested. Track surveys have been supplemented with indices of the number of bobcats run by dog hunters (Fig. 4) and sightings of bobcats by WDNR personnel (Fig. 5). The number of bobcats run by dog hunters has been positively correlated with track counts ( $n = 18$, $r = 0.56$, $P = 0.015$). In contrast, bobcat sightings by WDNR personnel have not been correlated with the other two indices (winter track count: $n = 17$, $r = -0.06$, $P = 0.82$; dog hunters: $n = 12$, $r = 0.28$, $P = 0.37$). Pilot studies have been conducted on a bowhunter wildlife observation survey, but to date the survey has not become operational.

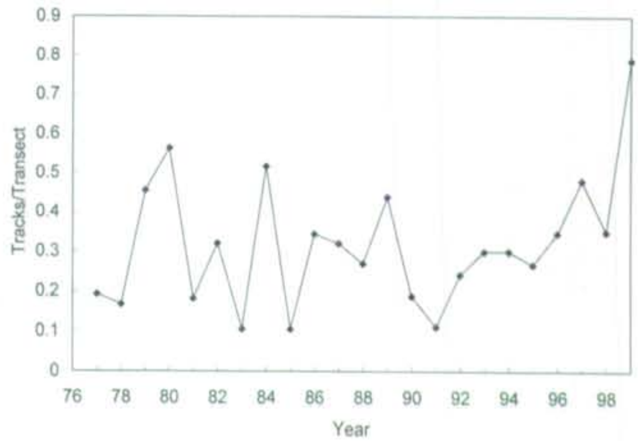


Fig. 3. Number of bobcat tracks/transect on winter track surveys in northern Wisconsin, 1977–99.

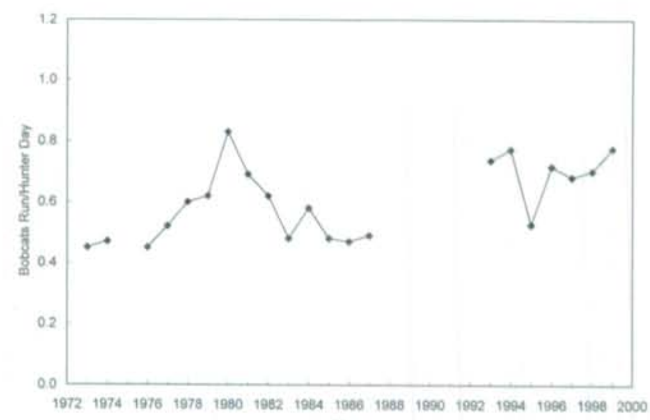


Fig. 4. Number of bobcats run/hunter day by successful hound hunters in Wisconsin, 1973–99.

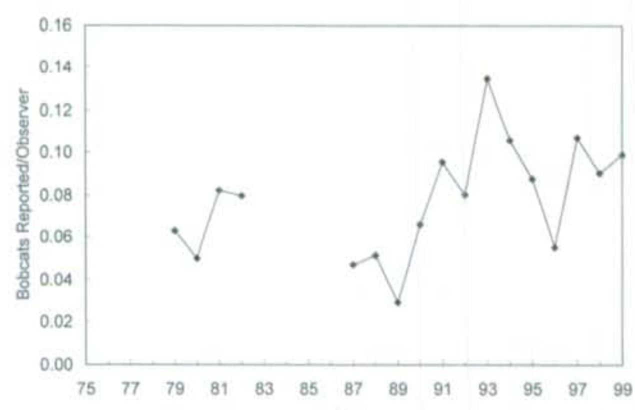


Fig. 5. Number of bobcats reported as observed by Wisconsin DNR personnel, 1979–99.

The WDNR continues to use the Minnesota furbearer model for modeling Wisconsin's bobcat population. The model combines information on the size and sex- and age-structure of the harvest with estimates of age-specific reproductive rates and non-harvest mortality rates. Mandatory carcass collections have provided information on harvest age- and sex-structure along with estimates of reproductive rate that are used as model inputs. Nearly 2,300 carcasses have been examined since 1983. Based on model simulations, we estimate that the fall bobcat population in northern Wisconsin has recently fluctuated from a low of about 1,500 in the mid-1980s to a high of about 2,200 in the last couple of years (Fig. 6). However, simulated population trends generated by the model are very sensitive to small changes in initial population size. The model is most useful when it can be calibrated to an independent trend index or to estimates of absolute population size. Because population density has only been estimated in one telemetry study of limited scope (Lovallo 1993) and questions remain about the accuracy of current indices, the results from the population model should be interpreted with caution.

Since 1980, the number of applicants for permits and number of permits issued have been annually documented. During 1973–89, successful bobcat harvesters were surveyed to estimate effort. Since 1993, all permit recipients have been surveyed to estimate their participation and effort in pursuing bobcats. The market value of bobcat pelts sold in Wisconsin is estimated annually via a survey of fur buyers. However, estimates of the number and value of bobcats pelts sold directly to Canadian auction houses are not currently available, nor are estimates of the number and value of taxidermy mounts. Although bobcats occur in a wide variety of habitats throughout their geographic range, in Wisconsin they are primarily limited to the northern third of the state. Lowland conifer stands and recent aspen clearcuts with abundant snowshoe hares appear to be their preferred habitat in Wisconsin. Forest inventory data are periodically reviewed to assess potential changes to bobcat habitat suitability. In addition, changes in the abundance of snowshoe hares are monitored with the winter track survey and harvest by small game hunters.

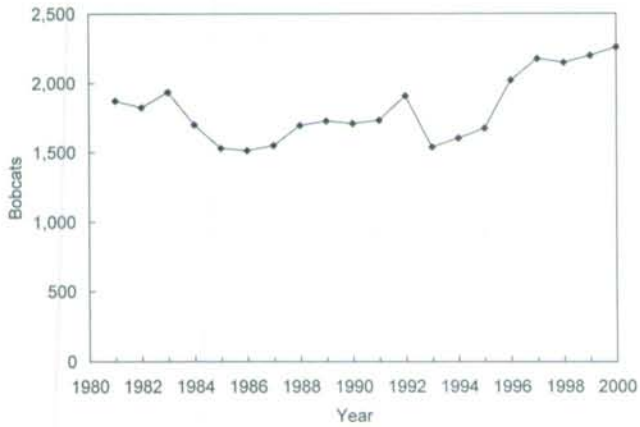


Fig. 6. Estimated trends in the Wisconsin bobcat population, 1981–2000, based on the Minnesota Furbearer Population Model.

The WDNR's Furbearer Advisory Committee annually reviews available population and harvest information and makes recommendations on future harvest and permit quotas. Because the Wisconsin Ojibwa tribes retained their rights to hunt, fish, and gather in the portion of northern Wisconsin that was ceded to the United States government in the mid-1800s, they are entitled to a portion of the allowable harvest. The tribes are represented on the Furbearer Advisory Committee by the Great Lakes Indian Fish and Wildlife Commission, whose staff assist the WDNR in reviewing population information and determining annual harvest quotas.

## CONCLUSIONS

During the past 40 years Wisconsin's management of bobcat harvests has evolved from unrestricted bounty payments to a carefully regulated limited quota system. These changes have been driven by reductions in the occupied range in Wisconsin, concerns about the status of bobcats within the WDNR, and changing public attitudes about the role of predators in ecosystems. Once considered a varmint, bobcats are now largely viewed as an important component of Wisconsin's northern forest and as a prized species by Wisconsin's hunters and trappers.

As harvest management strategies have become more restrictive during the past 40 years, the information needed to support management decisions has increased greatly. Wisconsin's harvest management system recently survived intense judicial scrutiny. However, the outcome of the story may have been different if the courts found that WDNR had the burden of proof to show that the population was stable.

Adequate monitoring of the relatively low-density bobcat population remains a challenge for resource managers. With this in mind, we have been carefully restricting harvest during the past decade to <220 bobcats/year to help ensure the long-term stability of the population. We recommend that the current population monitoring program and restrictive harvest strategies be continued. We also recommend the implementation of a bowhunter wildlife observation survey to strengthen the monitoring program.

## ACKNOWLEDGMENTS

We thank the many hunters, trappers, wildlife managers, and law enforcement personnel who provided much of the information on Wisconsin's bobcats during this period. We especially want to acknowledge W. A. Creed, J. E. Ashbrenner, and B. J. Dhuey who coordinated, analyzed, and interpreted the various bobcat studies and surveys during the past 30 years. C. M. Pils and R. L. Jurewicz coordinated the WDNR's response to the petition, reviewed an earlier draft of this manuscript, and provided many helpful comments. J. S. Christenson and P. Peterson provided legal council during the litigation. Funds for much of the research and surveys were provided through Federal Aid in Wildlife Restoration Project W-141-R.

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# PERSPECTIVES ON BOBCAT MANAGEMENT IN ILLINOIS

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***Abstract***: Long considered rare in Illinois, bobcats (*Lynx rufus*) were protected from harvest in 1972 and listed as a state threatened species in 1977. Recent (1995–99) studies showed a widespread distribution and a trend toward increasing relative abundance. About 30–40% of the state was classified as good to excellent habitat. Based on these findings, bobcats were removed from Illinois' list of state threatened species in 1999. Long-term (1992–98) trends in the Archer's Index were similar for Illinois, Indiana, and Missouri, suggesting that cooperative efforts to collect and analyze data might improve the precision of estimates for annual changes in abundance in the lower Midwest. Preliminary estimates of density, survival, and other demographics suggest that Illinois' population could sustain a limited harvest. While biological integrity is an important consideration, we recognize the fate of such a proposal will be decided by broader public policy.

***Key words***: bobcat, furbearer, Illinois, *Lynx rufus*, wildlife management.

The bobcat's (*Lynx rufus*) historic range extended from southern Canada to central Mexico (Hall and Kelson 1959). Early management programs afforded little protection and often included bounties (Hubert 1982, Phelps 1990, Stiver 1990) or predator control activities (Cain 1971, Melchior et al. 1987). Few changes occurred in the following decades. For example, Faulkner (1971) listed the bobcat as unprotected in 40 of the 48 conterminous United States and subject to bounties in 10.

Thirty-five states allowed the harvest of bobcats in 1976 (Deems and Pursley 1978), the same year a Presidential Executive Order created the Endangered Species Scientific Authority (ESSA) to oversee U.S. compliance with the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Johnson 1984). The ESSA's primary responsibility was to review applications for permits allowing the import or export of species listed in the treaty and determine whether trade was detrimental to their survival (Gluesing et al. 1986). Initially, information required by ESSA for a "no detriment" finding included population trends, harvest levels, distribution of harvest, and habitat evaluation (Gluesing et al. 1986, Rolley 1987). Few states could provide the information for bobcats, which were listed in Appendix II of the treaty and required a permit for export (Gluesing et al. 1986). This situation catapulted research and management activities (Dyer 1979, Berg 1990, Distefano 1990), as did rising fur prices and harvest levels (McCord and Cardoza 1982). For example, the average annual harvest of bobcats in the U.S. increased from about 10,000 in the 1950s and 1960s to 44,000 in the 1970s (Obbard et al. 1987) and peaked at >86,000 in 1979–80 (Novak et al. 1987).

This historical background is pertinent because research and management programs share a similar evolution and focus in most states. Ironically, many states that protected bobcats completely because of their rare status made comparatively little headway. Such was the case in Illinois, where bobcats were protected since 1972 (Illinois Revised Statutes 61, § 2.31). We describe recent efforts to upgrade Illinois' program, compare it to other states, and discuss some of the challenges and opportunities that lie ahead.

## HISTORICAL STATUS AND MANAGEMENT OF BOBCATS IN ILLINOIS

Bobcats were common and distributed widely in Illinois during the 1700s and early 1800s (Cory 1912, Hoffmeister 1989). They declined dramatically by the mid-1800s because of habitat destruction and unregulated harvest during European settlement (Mohr 1943). Considered rare by the early 1900s, bobcats were thought to occur in only a few of the southernmost counties (Brown and Yeager 1943).

Little was known about the bobcat's status in the mid-1900s except for occasional records that confirmed their presence (Thom 1981). Illinois' Endangered Species Protection Board listed the bobcat as a state threatened species in 1977. The designation probably reflected a paucity of data on the bobcat's status rather than any compelling evidence it was "likely to become endangered in the wild in Illinois within the foreseeable future" as defined by the Illinois Endangered Species Protection Act (§520 Illinois Compiled Statutes 10/2). The listing afforded additional protection under state law (§520 Illinois Compiled Statutes 10/3), but it also split responsibilities for management between "game" and "non-game" interests. As elsewhere (Alverez 1994), this organizational barrier hampered progress in research and management activities.

## RECENT MONITORING, RESEARCH, AND MANAGEMENT

Rhea (1982) compiled 89 reports of bobcat sightings from 52 counties during 1979–82. Few sightings were documented after Rhea's assessment (Herkert 1992), but anecdotal reports suggested that the bobcat's distribution and abundance increased during the mid- to late 1980s. This rekindled interest in the species' status. Early efforts to quantify observations began in the early 1990s and relied on existing data collection procedures. The Cooperative Wildlife Research Laboratory at Southern Illinois University at Carbondale later compiled this data and conducted field studies under a Federal Aid in Wildlife Restoration project. Objectives of the study, initiated in 1995, included: (1) determining the bobcat's relative abundance and distribution in Illinois, (2) mapping and estimating the area and relative quality of habitat types that support, or have potential to support, bobcat populations, and (3) developing criteria for assessing bobcat status in Illinois.

Standardized data on distribution and relative abundance were collected for the first time in 1991 as part of an Archer's Index. Hamilton et al. (1990) described the index, computed as the number of sightings per 1,000 hrs by archery deer hunters who volunteered to keep logs of their observations and activities. Sightings of bobcats were relatively infrequent and distributed unevenly, contributing to large confidence limits at sampling intensities adequate for other species (Ver Steeg and Warner 1997). While this limited our ability to detect annual changes in abundance, the method proved useful for monitoring long-term trends (Woolf and Nielsen 1999). For example, Hubert and Bluett (1999) reported a linear increase from 1992 (0.53 bobcat sightings/1,000 hrs) through 1998 (1.10 sightings/1,000 hrs).

We also collected sighting data from successful firearm deer and spring turkey hunters when they registered their kills at check stations. These sources provided 1,842 records during 1992–98 (Woolf et al. 2000). Sightings by successful firearm deer hunters were most common ($n = 1{,}447$), and increased from 0.35/1,000 hrs of effort in 1992 to 1.69/1,000 hrs of effort in 1998 (Woolf et al. 2000). Woolf and Nielsen (1999) noted that sightings by firearm deer hunters were a cost-effective way to monitor long-term trends in relative abundance but, like the Archer's Index, probably failed to provide an accurate measure of annual changes.

Sighting reports from archery and firearm deer hunters along with other sources were widespread, occurring in 99 of 102 counties (Gibbs 1998). Seventeen counties had >30 sightings from 1982 through 1998, considered indicative of a high resident population (Woolf et al. 2000). Thirteen of these counties were located in the southernmost portion of Illinois, 3 in the west-central part of the state, and 1 in extreme northwestern Illinois.

Two habitat models were constructed from sighting locations and digital landscape data. The first predicted presence or absence in a county based on proportion of woods, patch density of woods, and proportion of slope ≥18% (Woolf and Nielsen 1999). Another predicted the relative abundance of bobcats in a county using proportion of woods, proportion of slope ≥18%, and density of rural roads (Gibbs 1998). Outputs were consistent with independent sighting locations used for validation and suggested that bobcats occurred in moderate to high numbers in about 40% of the state (Woolf and Nielsen 1999). Habitat suitability models constructed with logistic regression predicted that 31% of Illinois offered good to excellent habitat distributed in a pattern similar to locations used for validation and that predicted by county-wide models (Woolf and Nielsen 1999). The models provided a resolution that was course (e.g., compared to those based on habitat preferences of radiocollared animals), but appropriate for planning and management activities, which are usually implemented at statewide or regional scales.

Radiocollared bobcats ($n = 96$) provided reliable information on movements, survival, social organization, and other demographics (Kennedy 1999, Woolf and Nielsen 1999). The project was continued in 1999 with the following new objectives: (1) estimate the number of bobcats living south of Interstate 64, (2) evaluate or develop population models capable of detecting changes in bobcat abundance and provide estimates of input variables, and (3) determine population genetics of bobcats in the central United States. We believe that this body of work will set a solid foundation for state and regional conservation efforts.

Bobcats were removed from Illinois' list of state threatened species in April 1999 (17 Illinois Administrative Code, Chapter I, Section 1010). They are currently protected by the Wildlife Code (§520 Illinois Compiled Statutes 5/2.2), which prohibits hunting and trapping of this species (§520 Illinois Compiled Statutes 5/2.30).

## COMPARISONS WITH OTHER STATES

Woolf and Hubert (1998) reported that 10 states prohibited the harvest of bobcats in 1996. Pennsylvania will offer a limited harvest season in 2000–01 (V. Ross, Pennsylvania Game Commission, personal communication), leaving Illinois among a dwindling minority. Despite this distinction, many of our research and management objectives parallel those expressed by managers in other states (Table 1).

Lacking any direct measure of bobcat densities over large geographic areas, managers have turned to surveys and indices of abundance (Table 2). Validation and precision of these methods are as much a concern today as they were in the past (McCord and Cardoza 1982), so most states (94%) use ≥2 methods as recommended by Rolley (1987). Illinois' use of hunter/trapper surveys, sighting reports, and an archer's index is typical of the region. Methods used by adjacent states (IN, KY, WI, MO, IA) include sighting reports ($n = 4$), archer's indices ($n = 2$), employee opinions ($n = 2$), hunter/trapper survey ($n = 1$), scent station index ($n = 1$), road-kill survey ($n = 1$), sign/track survey ($n = 1$), and prey survey ($n = 1$) as well as methods linked directly to harvest ($n = 5$) (A. Woolf, unpublished data).

Table 1. Research and management needs identified by bobcat managers in the conterminous United States[a], 1996 (A. Woolf, unpublished data).

| Rank | Research needs | Management needs |
|---|---|---|
| 1 | Reliable survey methods | Control harvest to better match geographic/temporal difference in abundance |
| 2 | Demographics (e.g., mortality, recruitment) | Monitor abundance |
| 3 | Distribution and abundance | Protect or improve habitat |
| 4 | Habitat availability and use | Improve public knowledge of and support for managemennt activities |
| 5 | Interactions with coyotes and other carnivores | Evaluate effectiveness of/need for federal oversight |

[a]State agencies were surveyed as described by Woolf and Hubert (1998).

Table 2. Methods used to monitor the abundance of bobcats in the conterminous United States[a], 1996 (A. Woolf, unpublished data).

| Method | No. of states |
|---|---|
| Hunter/trapper surveys | 31 |
| Harvest data (e.g., catch per hunter/trapper, pelt sales/ tagging) | 26 |
| Employee opinion | 20 |
| Sighting reports | 19 |
| Life table analysis | 13 |
| Computer population model | 13 |
| Archer's Index | 8 |
| Sign/track survey | 8 |
| Scent station survey | 6 |
| Prey survey | 4 |
| Spotlight survey | 2 |
| Landowner/rural mail carrier survey | 2 |
| Mark-recapture | 1 |
| Road-kill survey | 1 |
| Incidental catches | 1 |
| Bobcats taken by damage control agents | 1 |
| Summer roadside survey | 1 |
| Radiotelemetry and habitat mapping | 1 |

[a]State agencies were surveyed as described by Woolf and Hubert (1998).

## PERSPECTIVES ON MANAGEMENT

Monitoring the abundance of bobcats is a key activity and concern of managers in most states. Our research contributed little in the way of new approaches for accomplishing this task. However, we demonstrated similar long-term trends for independent results of the Archers Index and surveys of firearm deer hunters. Some critics might argue that neither method has been validated against populations of known size. We believe this expectation is unrealistic because estimating population size with methods like mark-recapture is neither practical nor appropriate for geographic scales best suited for comparisons (i.e., statewide or possibly by management zone, each of which encompasses >50,000 km$^2$).

While we are confident in the ability of these techniques to detect long-term, statewide trends in the relative abundance of bobcats, especially when used together or with other indices, we recognize that neither the Archers Index nor surveys of firearm deer hunters appear suitable for tracking local or annual fluctuations. Increasing our sample size to improve precision is not an option for surveys of successful firearms deer hunters because we presently collect data from all successful hunters when they register their kills ($n$ = 95,608 in 1998). Mail surveys of unsuccessful hunters might be possible, but we suspect differences in timing and methodology would preclude the use of these data to augment those collected at check stations.

Hamilton et al. (1990) estimated sample sizes and costs needed to obtain specified levels of precision with the Archers Index. They concluded that desired levels of precision could be obtained for bobcats at the statewide level and in some, but not all, regions of the state. We suggest that a similar approach would be useful for determining whether data from Illinois, Indiana, and Missouri (Table 3) might collectively provide a more precise and cost-effective way to monitor annual changes in abundance than individual efforts. Other managers have noted apparent changes in abundance that occurred on large (i.e., multi-state) geographic scales (Fox et al. 1990), lending credence to the theory that cooperative efforts to monitor annual fluctuations and long-term trends might be meaningful as well as convenient.

One of the greatest changes in the past 20 years has been a fundamental shift in social and political attitudes toward our role as managers (Sparrowe 1995). Once viewed as a tenet in decision-making, good science has given way to greater public involvement (Decker and Chase 1997). Managers are now faced with international treaties (Hamilton et al. 1998), citizen-sponsored ballot measures (Minnis 1998), litigation (Olson 1995), legislation (The Wildlife Legislative Fund of America 1999), and public opinion (Andelt et al. 1999, Manfredo et al. 1999) as well as their traditional responsibilities. Based on research (Woolf and Nielsen 1999, Woolf and Heist 2000), which shows a widely distributed, increasing population currently at moderate densities (preliminarily, a minimum estimated density of 0.27 bobcats/km$^2$ in the southern part of the state), we believe that bobcats could sustain a limited harvest in Illinois. Implementing a harvest season is consistent with state statutes that authorize and encourage the Department of Natural

Table 3. Archer's Index for bobcats in Illinois, Indiana, and Missouri, 1992–98.

| | (No. bobcats sighted/1,000 hrs) | | |
|---|---|---|---|
| Year | Illinois[a] | Indiana[b] | Missouri[c] |
| 1992 | 0.53 | 0.30 | 2.92 |
| 1993 | 0.65 | 0.26 | 3.16 |
| 1994 | 0.40 | 0.43 | 3.36 |
| 1995 | 0.81 | 0.60 | 3.77 |
| 1996 | 0.80 | 0.88 | 4.09 |
| 1997 | 1.34 | 1.00 | 4.45 |
| 1998 | 1.10 | 0.89 | 4.36 |

[a]Hubert and Bluett (1999).
[b]L. Lehman, Indiana Department of Natural Resources, personal communication.
[c]Hamilton and Fantz (1999).

Resources to provide opportunities for regulated hunting and trapping (§520 Illinois Compiled Statutes 5/1.3, §20 Illinois Compiled Statutes 801/1-15). However, we decline to speculate on the outcome of such a proposal in a legislative forum that can be influenced as much or more by public policy than biological integrity.

Forest cover types are an integral part of the bobcat's ecology in Illinois (Gibbs 1998, Woolf and Nielsen 1999, Woolf and Heist 2000). These habitats have increased by 41% since 1926 (Illinois Department of Energy and Natural Resources 1994), and currently comprise about 1.6 million ha, or 11.3% of the state (Illinois Department of Natural Resources 1996). While classified as wetlands, bottomland forests and swamps comprise an additional 328,000 ha (Illinois Department of Natural Resources 1996). The density of forest cover types is greatest in the southern part of the state and along the Illinois and Mississippi rivers (Illinois Department of Natural Resources 1996), especially where poor soils and steep terrain discourages land use like agriculture (Roseberry and Woolf 1998). Large (>200 ha) tracts of forest are rare in Illinois (Holland et al. 1972), leading Robinson (1991) to characterize forest tracts as "small, isolated, and dominated by edge habitats." Ownership is mostly private (>90%), and comprised of small ($\bar{x}$ = 8.6 ha) parcels (Iverson 1991) maintained predominantly for recreation or aesthetics (Young et al. 1984, Hubert et al. 1999).

Direct loss of habitat is not an immediate concern because recent trends show stable to slightly increasing amounts of forest cover (Iverson et al. 1989). Some emerging issues that might affect habitat suitability include the spread of exotic, invasive species, residential development, and changes in dominant cover types (Illinois Forestry Development Council 1999). Maples (*Acer* spp.) and other shade-tolerant species are replacing traditional oak-hickory (*Quercus-Carya*) communities, especially on mesic sites (Ebinger 1986, Nelson and Sparks 1998). This conversion has been dramatic, with a 41-fold increase in the acreage of maple forests since 1962 (Illinois Department of Energy and Natural Resources 1994). Probable causes include fire suppression and inadequate use of silvicultural practices needed for regeneration of oaks (Parker 1989, Abrams 1992, Roovers and Shifley 1997, Larson et al. 1999).

Many ecologists (e.g., Graber and Graber 1976) consider maple forests less suitable for wildlife than oak-hickory communities. While we agree and encourage more active management of Illinois forests to maintain their productivity and diversity, we recognize that our position is not supported by any direct evidence that prevailing trends are detrimental to bobcats. Studies in forested landscapes suggest that a diversity of tree species and age classes is beneficial for bobcats, mainly because prey availability is greatest in heterogenous habitats (Hall and Newsom 1978, Miller 1980, Hamilton 1982, Rolley and Warde 1985, Leopold et al. 1995). We hesitate to apply these findings directly to a landscape characterized by small tracts (< 50 ha) of forest cover. For example, conversion of oak-hickory communities to those dominated by maples might have a negligible effect on bobcats if forest cover is more important structurally than for prey, which bobcats obtain in nearby grasslands and agricultural fields. Experimental application of silvicultural practices (e.g., controlled burning, timber stand improvement, group or shelterwood harvest systems) and long-term, broad-based monitoring of responses by flora and fauna, including animals at high trophic levels like the bobcat, would help to resolve this uncertainty and guide public policies on management of fragmented forests.

Illinois' bobcat management program is a work in progress. To date, we have established the bobcat's range, relative abundance, and habitat distribution in the state. Ongoing research will provide modeling capabilities that incorporate estimates of the bobcat's density and demographics in the southern part of the state. Collectively, this information exceeds legal and professional standards previously proposed for management of bobcats (Gluesing et al. 1986, Mech 1978). Our efforts yielded little in the way of new strategies or tools for managing bobcats, but we are encouraged by the possibilities of cooperative efforts to monitor their relative abundance in the lower Midwest. Given a stable to increasing population and habitat base, the prospects for a regulated harvest appear good from a biological perspective. However, such a proposal is likely to be controversial and its outcome will be determined in public forums that preclude a forecast. Sentiments expressed by Leopold (1933:vii) seem relevant given recent attempts to prohibit the harvest of bobcats in his home state of Wisconsin (Olson 1995), "The conservation movement has sought to restore wild life by the control of guns alone, with little visible success. Management seeks the same end, but by more versatile means."

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# STATUS AND MANAGEMENT OF BOBCATS IN PENNSYLVANIA

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***Abstract*:** Bobcats (*Lynx rufus*) were widely harvested in Pennsylvania prior to their protection in 1970. During the past 30 years, bobcat populations have expanded geographically and numerically throughout the state and hunters and trappers have expressed interest in participating in a limited bobcat harvest season. The Pennsylvania Game Commission has conducted intensive research and monitoring programs since 1985 designed to assess habitat relationships and availability and detect changes in bobcat distribution and relative population levels. A recent assessment of harvest feasibility suggested a limited number of bobcats could be harvested from high density regions while maintaining stable to increasing bobcat populations. Current monitoring and harvest management procedures are discussed.

***Key words*:** bobcat, distribution, harvest, *Lynx rufus*, population monitoring.

Public attitudes concerning predators and the management of the bobcat (*Lynx rufus*) in Pennsylvania have changed dramatically during the last century. Bobcats and other predators were considered vermin in the 1700s and 1800s. As early as 1819 a $1 bounty was established to promote the harvest of bobcats in the commonwealth. This bounty was increased to $15 during 1916 and >7,000 bobcats were killed for bounty during 1916–37 (Fig.1). A realization that bounties were ineffective for controlling predator populations resulted in the removal or reduction of bounties on many predators. The bounty was removed from bobcats in 1937, but they remained unprotected and were widely harvested until classified as a game animal in 1970. This reclassification occurred in response to concerns for bobcat populations and was implemented to allow populations to expand throughout the commonwealth. Reclassification empowered the Pennsylvania Game Commission (PGC) to set regulations to manage bobcat populations. There was no legal harvest of bobcats in Pennsylvania during 1970–99.

During the past 15 years, Pennsylvania trappers and hunters have witnessed dramatic geographic and numeric expansion of bobcat populations and have continually requested PGC to assess harvest feasibility. Sixty percent of 2,056 licensed furtakers surveyed during 1994 indicated they would like to participate in a regulated bobcat harvest season (Lovallo 2000). During this period, the PGC conducted intensive field research to assess factors affecting bobcat density and distribution, and implemented surveys and carcass collection programs to monitor distribution and to assess population characteristics. Here, I summarize information contained in a recent version of PGC's bobcat management plan (Lovallo 2000). Annual management, research, and harvest recommendations have focused on the PGC bobcat management goals to maintain, conserve, and promote sustainable bobcat populations in regions of Pennsylvania that provide suitable habitat conditions and to provide recreational opportunities for consumptive and non-consumptive users of bobcats (Lovallo 2000).

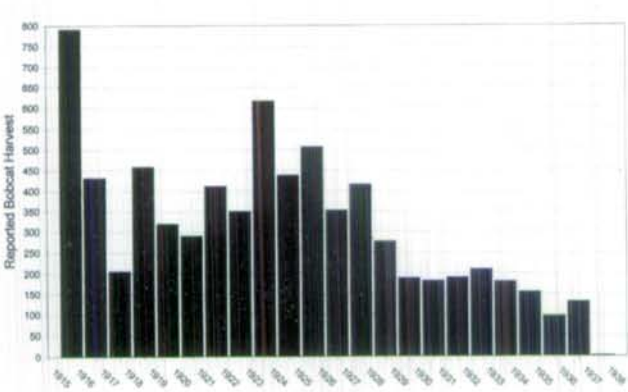


Fig 1. Numbers of bobcats harvested for bounty in Pennsylvania during 1916–38.

During April 2000, the PGC board of commissioners approved a highly regulated and limited bobcat harvest season to be conducted in select regions of the commonwealth. This bobcat hunting and trapping season provided Pennsylvanians with their first opportunity to harvest a bobcat in the state since 1970. Herein, I summarize survey data and research results as they relate to the assessment of bobcat harvest feasibility.

## DISTRIBUTION

The geographic range of bobcats includes most of the contiguous United States, with the exception of major agricultural regions of the Midwest, and Mexico (Anderson 1987). Pennsylvania's bobcat population is important regionally as it provides a critical link between established populations in New York to those of West Virginia, Virginia, and southern Ohio. Recent reports of bobcat abundance and distribution in Pennsylvania suggest that established populations extend throughout the northern, central, and southwest regions and that the range of established populations has increased since 1970 (Giles 1986, Merritt 1987, Lovallo 1999) (Fig. 2).

## POPULATION STRUCTURE

Because there was no legal harvest of bobcats in Pennsylvania during 1970–99, the majority of PGC's data regarding population structure came from vehicle-caused bobcat mortalities. The sex ratio of bobcats collected in Pennsylvania due to bobcat-vehicle mortalities during


Fig. 2 Wildlife Conservation Officer estimates of bobcat distribution and population status in Pennsylvania during 1998.

1986–1999 was 1:1, whereas sex ratio estimates from harvested bobcat populations typically show a preponderance of males (Anderson 1987).

The proportion of yearlings in a bobcat population is closely related to the intensity of harvest and may result from high reproduction or high adult mortality (Anderson 1987). In harvested populations, the percentage of yearlings in the harvest sample generally exceeds 50% and may reach 76% in areas of relatively low bobcat density and high harvest pressure (Fredrickson and Rice 1979). Lembeck and Gould (1979) estimated 16% yearling composition in an unharvested population in California, compared to 43% yearlings in a harvested population occurring in similar habitats. Analyses of the age distribution of Pennsylvania's bobcat population suggest that <20% of the bobcat population are yearlings (Fig. 3). Age distributions for males and females were similar. Age-distribution data and the occurrence of older individuals (>10 yr) in the population are consistent with that of an unharvested population.

## MORTALITY

The primary cause of bobcat mortality, in both harvested and unharvested populations, is usually human-related (Anderson 1987). Predation, from coyotes (*Canis latrans*), wolves (*Canis lupus*), and mountain lions (*Felis concolor*) has been reported, but is rare. Instances of cannibalism have also been reported (Gashwiler et al. 1961, Litvaitis et al. 1984), and several studies reported bobcat mortalities resulting from porcupine quills (Fuller et al. 1985). Bobcats are susceptible to a variety of diseases including rabies and panleukopenia (feline distemper). Fox (1982) reported that panleukopenia may be a significant mortality factor for bobcats in southern New York. Although cases of rabies and panleukopenia have been documented in Pennsylvania, the impact of disease on the bobcat population is unknown. During the past 30 years, vehicle collisions were likely the primary source of bobcat mortality in Pennsylvania. The majority of vehicle-caused bobcat mortality occurred during September through November (Lovallo 1999).

Age-distribution data from road-killed bobcats in Pennsylvania suggest that adult survival rates range from 50–87% until age 5 when survival increases to greater than 80% and remains constant (Fig. 3). Annual estimates of adult survival typically range from 50–70% in harvested populations (Anderson 1987). Because survival estimates are often calculated from harvest-related data, there are very few reports from unharvested populations. However, Bailey (1974) reported 97% annual survival in an unharvested population in Idaho.

There is evidence of sex-related differences in survival in harvested bobcat populations; male survival is generally lower than females, particularly during the first

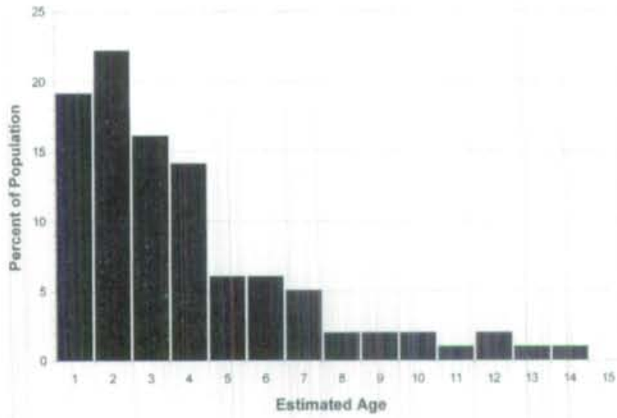


Fig. 3. Estimated age distribution of bobcats in Pennsylvania during 1986–99.

several years. Males may be more susceptible to human-related mortality because of their extensive movements and larger home ranges. Knick (1990) found the proportion of males in the harvest increased throughout the harvest season and attributed this to increased movement by males prior to breeding. The 1:1 sex ratio observed for vehicle-caused bobcat mortalities in Pennsylvania did not suggest that sex-specific differential mortality is occurring.

## POPULATION MODELING

The PGC developed a bobcat population model to project population growth and to assess the potential impact of regulated harvest. Age-specific survival and fecundity were estimated from field research studies in Pennsylvania or from available bobcat literature. When a range of parameter estimates was available, the most conservative estimate was used (e.g., low survival and fecundity).

Initial population estimates (population size at time 0) were determined from habitat suitability estimates (Table 1), analyses of potential female home ranges, and statewide distribution data based on surveys of field personnel, incidental captures, and vehicle-caused bobcat mortalities. The model considered a maximum 80% occupancy rate of suitable habitats within potential female home ranges in areas (i.e., Wildlife Conservation Officer districts) known to support established bobcat populations . Based on these methods, we determined an initial population size of 3,156 adult resident bobcats. Initial estimates of population size were conservative; the PGC has substantial evidence (observations, vehicle-caused mortalities, and incidental captures) that bobcats currently occupy habitats beyond the geographic extent identified in these analyses.

Age-specific survival rates for adult bobcats were estimated from age distribution data collected from vehicle-caused bobcat mortalities (Crowe 1975). The population model used a 33% survival rate for juveniles. This rate was based on values in the literature and is thought to be very conservative for an unharvested population. Age-specific fecundity was estimated from available literature on litter size and pregnancy rates. The bobcat population model used a 65% pregnancy rate and a mean litter size of 1.5 kittens for yearling bobcats (<2 yr) and an 80% pregnancy rate and mean litter size of 2.5 kittens for adult bobcats (≥2 yr).

The population model incorporated stochastic parameters to develop confidence intervals for model projections. The model used a coefficient of variation to express the variation of vital parameters. The coefficient of variation was based on a standard deviation of ±5% of parameter estimates. The model also considered demographic stochasticity (variations in sex ratios and age distributions) in model output. The model was replicated 500 times to assess stochastic effects.

The population model indicated that Pennsylvania's bobcat population is increasing at an annual rate of ≥4–6%. The population model assumed no compensatory (density-dependent) response to increased mortality due to harvest although the potential for a compensatory response exists. Also, the model considered harvest mortality to be 100% additive to other causes (e.g., vehicle-caused mortalities). Simulated effects of varying harvest levels on population growth indicated that a harvest of <220 adult bobcats would result in stable to increasing populations. These procedures served as the analytical basis for the establishment of an annual harvest objective of 175 bobcats during initial seasons.

Table 1. Predicted area (km$^2$) of suitable habitat for male and female bobcats and percent composition of female habitat and potential female home range area (km$^2$) within Pennsylvania Game Commission Furbearer Management Units in Pennsylvania.

| Unit | Unsuitable habitat | Suitable habitat | | | | |
|---|---|---|---|---|---|---|
| | | Male only | Male and female | Female only | Total female(%)[a] | Potential female home range area (%)[a] |
| 1 | 7,378 | 1,767 | 1,313 | 165 | 1,478 (12) | 1,019 (8) |
| 2 | 12,253 | 5,257 | 4,575 | 523 | 5,099 (18) | 7,952 (29) |
| 3 | 7,946 | 3,127 | 3,263 | 426 | 3,689 (20) | 6,851 (37) |
| 4 | 17,787 | 4,324 | 3,625 | 576 | 4,201 (14) | 2,427 (8) |
| 5 | 12,765 | 4,159 | 3,584 | 604 | 4,188 (17) | 5,888 (23) |
| 6 | 16,381 | 2,799 | 2,204 | 497 | 2,701 (11) | 2,137 (9) |

[a]Percent of Furbearer Management Unit.

## POPULATION MONITORING

### Survey of Wildlife Conservation Officers

The PGC used a combination of mail surveys and field methods to monitor the range of established bobcat populations and to assess bobcat population trends. For law enforcement efforts, 67 Pennsylvania counties are divided into 135 Wildlife Conservation Officer (WCO) districts. The Furbearer and Farmland Wildlife Section of the Bureau of Wildlife Management surveys WCOs periodically concerning evidence relating to the status, distribution, and population trends of bobcats in their respective districts. The survey is mailed to WCOs after trapping seasons to insure that incidental captures attributed to trapping are reported. In districts where WCOs were relatively new, they were advised to request information from the previous WCO or from WCOs in surrounding districts.

During the most recent survey (1998), bobcat populations were reported as stable within 59 districts (49%), increasing within 36 districts (30%), and declining in 1 district (<1%). Nineteen of 35 districts in northcentral and northeastern regions (Furbearer Management Zones 2 and 3) reported increasing bobcat populations. (Fig. 4)

### Vehicle-caused Mortalities

Wildlife Conservation Officers use a standardized kill report form to provide information on observed bobcat mortalities (e.g., vehicle-caused, illegal harvest, disease). When possible, carcasses are collected and examined to determine sex and age and to estimate productivity. The PGC uses a 3-year running average to monitor changes in the number of vehicle-caused mortalities (Fig. 5). A running average approach is used to temper effects of WCO position vacancies. There has been a steady increase in the number of reported vehicle-caused mortalities each year since this effort began in 1986.

### Game Take Surveys

The PGC uses a mail survey to poll approximately 2% of licensed hunters and 10% of licensed furtakers to assess hunter and trapper effort and to estimate harvest rates. During recent years, furtakers were asked to report the number of bobcats captured incidentally in traps set for other furbearers. There has been a general increase in the numbers of bobcats captured and released during 1990 to present (Table 2). If the number of bobcats captured per trapper is extrapolated to all licensed trappers, these surveys suggest that since 1994 trappers captured and released from 460 to >1,000 bobcats annually.

### Winter Track Counts

The PGC has developed a winter track survey that will be conducted by cooperators along fixed survey routes in Furbearer Management Zones 2, 3, and 5 beginning during 2000–01. Pilot projects of winter track counts were initiated in northeastern Pennsylvania during 1999 to train personnel and to develop effective protocols for statewide survey implementation. Pennsylvania Game Commission staff detected bobcat tracks along each route surveyed and encountered 17 unique sets of bobcat tracks during 4 pilot surveys. The mean detection rate was 0.27 tracks/km surveyed. Bobcat detection rates for each of the 4 surveys were: 0.25, 0.13, 0.19, and 0.50, respectively. For comparison, mean detection rates for coyote, fisher (*Martes pennanti*), and gray fox (*Urocyon cineroargenteus*) were 0.17, 0.08, and 0.03, respectively.

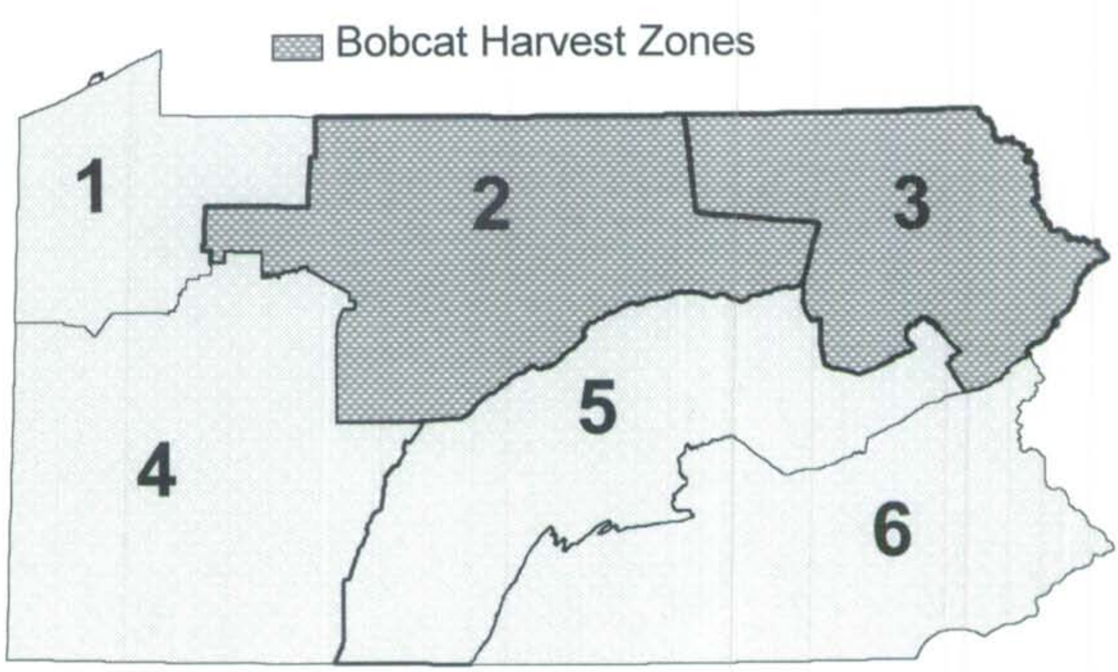


Fig. 4. Furbearer management zones and year 200 bobcat harvest zones in Pennsylvania.

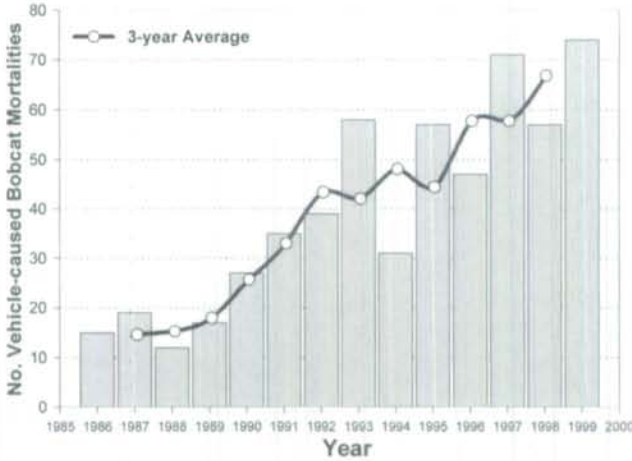


Fig. 5. Reports of vehicle-caused mortalities in Pennsylvania during 1986–99.

## HARVEST REGULATION

During April 2000, the PGC adopted a permit-based quota system to regulate the harvest of bobcats by hunters and trappers in the commonwealth. Under this system, the annual permit allocation was to be determined annually as the product of the harvest success rate (estimated from the previous year) and a harvest objective based on habitat assessment, annual evaluation of abundance indices, and annual refinements to the bobcat population model. An initial 2000–01 permit allocation of 290 permits was based on a harvest objective of 175 bobcats and a conservative 60% estimate of harvest success by permit holders. During the 2000–01 hunting and trapping seasons, harvest was restricted to Furbearer Management Zones 2 and 3 in northcentral and northeastern Pennsylvania. The daily possession limit and season bag limit was set as 1 bobcat by permit only. Because bobcats are regularly captured incidentally in traps set for other legal furbearers and because participation was limited by permit allocation, the bobcat harvest season was set concurrent with coyotes, foxes, opossums, raccoons, skunks, and weasels (mid-Oct to mid-Feb).

Applicants for 2000–01 bobcat harvest permits were required to purchase a furtaker license and to submit a $5 non-refundable application fee. A total of 3,274 applications were received and 290 permits were randomly allocated by public drawing during early September 2000. The PGC included a survey on the application form to assess hunter and trapper characteristics. Eighteen percent of applicants indicated that this was the first year they had purchased a furtaker license and 12% indicated they had bought a furtaker license primarily to apply for a bobcat permit. When asked to report their intended method of harvest, 63% indicated they would employ trapping, 55% indicated predator calling techniques, and 6% indicated hunting with dogs. Twenty-eight percent indicated they had experience hunting or trapping bobcats in other states or had experienced incidental bobcat captures in Pennsylvania.

Successful permit applicants received a bobcat harvest permit and a carcass tag to be attached to the bobcat immediately upon possession. Under current regulations, this tag must remain attached to the bobcat until the pelt is sealed by a commission representative prior to 10 days after the season close. Sealing consists of application of a permanent locking PGC pelt tag as well as a CITES export tag (the PGC received CITES export status for bobcat during October 2000). All bobcat carcasses are currently being collected for research purposes and will be used to refine reproductive estimates and to assess harvest effects.

## REGIONAL AND ECONOMIC SIGNIFICANCE

The conservation and management of Pennsylvania's bobcat population is of interest to hunters, trappers, and non-consumptive users alike. Bobcats are a highly regarded carnivore and represent the essence of wilderness for many people. Because bobcats are secretive predators and are rarely observed in the wild, seeing a bobcat in Pennsylvania's forests heightens the wilderness experience sought by outdoor enthusiasts (e.g., hikers, bird watchers, campers).

Table 2. Numbers of incidental bobcats captured and released as estimated by the Pennsylvania Game Commission Furtakers Survey.

| Year | No. survey respondents | No. furtaker licenses sold | No. bobcats released | Projected no. bobcat captures |
|---|---|---|---|---|
| 1990–91 | 2,302 | 20,377 | 40 | 354 |
| 1991–92 | 2,361 | 20,215 | 24 | 205 |
| 1992–93 | 1,652 | 20,345 | 26 | 320 |
| 1993–94 | 2,175 | 19,246 | 16 | 142 |
| 1994–95 | 2,056 | 21,905 | 101 | 1,076 |
| 1995–96 | 2,181 | 21,840 | 46 | 460 |
| 1996–97 | 2,363 | 25,636 | 62 | 673 |
| 1997–98 | 2,233 | 27,413 | 46 | 565 |
| 1998–99 | 2,466 | 25,877 | 108 | 1,133 |
| 1999–2000 | 1,557 | 17,414 | 62 | 693 |

Bobcat depredation on pets or livestock is uncommon in the northeastern U.S., but there have been reports of depredation on domestic cats and poultry. In the western U.S., bobcat depredation is thought to comprise <10% of all livestock losses (Virchow and Hogeland 1994). Bobcat harvests in North America produce up to 28,000 pelts annually valued at approximately $820,000. Approximately 3,200 bobcats, valued at $75,000, are harvested annually in the northern U.S. and upper Midwest. Bobcat pelts are used for coats, trim, and accessories, with the spotted fur of the belly being most valuable. Many hunters and trappers have indicated they would mount via taxidermy or tan the pelt of the first legal bobcat they harvest.

## CONCLUSIONS

Bobcat populations in Pennsylvania have persisted and prospered under a wide spectrum of management approaches over the past century. These approaches included unlimited harvest prior to 1970 (a period of population declines), complete protection during 1970–99 (a period of geographic and numeric population expansion), and highly limited and regulated harvest beginning in 2000. Recent assessments of harvest feasibility suggest that a limited number of bobcats can be harvested while maintaining stable to increasing bobcat populations on a statewide basis. The PGC has adopted a conservative approach to harvest implementation and is continuing efforts to monitor trends in bobcat distribution and relative density.

## ACKNOWLEDGMENTS

I thank the many biologists, Wildlife Conservation Officers, and volunteers who participated in the research described in this report. In particular we thank Jack Giles, who coordinated bobcat field research during 1985–97. Bobcat habitat suitability models resulted from a cooperative effort among the Pennsylvania Game Commission, The School of Forest Resources at The Pennsylvania State University, and The Pennsylvania Cooperative Fish and Wildlife Research Unit.

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# ABSTRACTS

## CHANGES IN SPACING PATTERNS WITH INCREASING POPULATION DENSITY OF AN INSULAR REINTRODUCED BOBCAT POPULATION

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***Abstract*:** We reintroduced bobcats (*Lynx rufus*) to Cumberland Island, Georgia, USA, and monitored their spacing patterns as we increased population density. In 1988 we introduced 14 bobcats, and in 1989 we reintroduced an additional 17 bobcats. During 1989–91, bobcat densities increased from 0.13 to 0.35 bobcats/km$^2$. We used the delta statistic (average distance between all possible pairs of locations) as a measure of home range size. For bobcats reintroduced in 1988, we found no trends in annual home range size over years ($P = 0.28$), but male home ranges were larger than female home ranges ($P = 0.01$). For bobcats reintroduced in 1989, we detected little evidence of a trend in home range size ($P = 0.07$) and no difference between sexes ($P = 0.75$). An index to intrasexual home range overlap indicated no change in home range overlap among bobcats reintroduced in 1988 ($P = 0.29$); however, the index showed a decline in home range overlap among bobcats reintroduced in 1989 ($P < 0.01$). We found that bobcats exhibited spacing patterns consistent with a prior-rights land tenure system, but they did not maintain exclusive home ranges. Consequently, we had no evidence that exclusive home ranges could serve as a mechanism to regulate population size.

## DEER HERD TRENDS, BOBCAT FOOD HABITS, AND VEGETATION CHANGE OVER 18 YEARS ON CUMBERLAND ISLAND, GEORGIA

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***Abstract*:** We released bobcats (*Lynx rufus*) on Cumberland Island National Seashore during 1988 and 1989 to restore an extirpated predator to the island. We monitored prey abundance and use during 1988–90. During 1997–98, we repeated the prey use surveys. We also analyzed white-tailed deer (*Odocoileus virginianus*) harvest data collected during 1980–97, repeated deer abundance surveys, and repeated measurements of live oak (*Quercus virginiana*) recruitment at plots established in 1985. During 1988–90, white-tailed deer comprised 20–38% of the seasonal diet of bobcats. During 1997–98, white-tailed deer comprised only 7–31% of bobcats' diets. Deer abundance indices decreased after the reestablishment of bobcats on Cumberland Island, and eviscerated weights of all deer age-sex classes except yearling females increased. After no significant change in height during 1986–89, mean oak sprout heights doubled between 1989 and 1997, and sprout densities increased. Our results are consistent with the hypothesis that predation by bobcats on white-tailed deer caused a decline in deer densities on Cumberland Island, which resulted in increased deer size and a release of vegetation from browsing pressure.

# AUTHOR BIOGRAPHICAL SKETCHES

### Bobcat research and management: have we met the challenge?

ALAN WOOLF is the director of the Cooperative Wildlife Research Laboratory (CWRL) and a professor of zoology at Southern Illinois University at Carbondale. He received his B.S. degree from Cornell University, his M.S. degree from Colorado State University, and returned to Cornell for his Ph.D. Alan's research interests are varied, but his professional emphasis centers around graduate programming, research, and education. He has served the CWRL for the past 21 years and has been director since 1987.

CLAY NIELSEN is a post-doctoral research fellow at the Cooperative Wildlife Research Laboratory at Southern Illinois University at Carbondale, where he received his Ph.D. studying habitat use and population dynamics of bobcats. Clay received his B.S. in Natural Resources at the University of Nebraska-Lincoln and his M.S. in Environmental and Forest Biology at State University of New York, College of Environmental Science and Forestry. Clay recently co-founded a consulting business called Holterra Wildlife Management that provides communities with management plans for wildlife.

### Multivariate models of bobcat habitat suitability for Pennsylvania landscapes

MATTHEW J. LOVALLO is furbearer biologist with the Pennsylvania Game Commission. Matt received a Ph.D. in Wildlife and Fisheries Science at The Pennsylvania State University where his doctoral work addressed the use of remotely sensed data and geographic information systems to model bobcat habitat suitability in Pennsylvania.

GERALD (Jerry) L. STORM (retired) is a former wildlife biologist with the Biological Resources Division, USGS, and the U.S. Fish and Wildlife Service, and Adjunct Associate Professor of Wildlife Managementt at The Pennsylvania State University. He received a Ph.D. in Ecology from the University of Minnesota. His research interests are in wildlife and habitat interactions and linkages between landscape use and conservation of biotic resources.

DAVID KLUTE is currently Assistant Non-game Migratory Bird Coordinator for the USFWS in Denver. He received a Ph.D. from The Pennsylvania State University, an M.S. from Kansas State University, and a B.S. from the University of Missouri. His interests include avian conservation and management and the incorporation of spatial dependence into habitat models.

WALTER TZILKOWSKI has been a Professor of Wildlife Science at The Pennsylvania State University since 1978. Dr. Tzilkowski teaches wildlife management, population dynamics, and biometrics.

### Impacts of reestablished fishers on bobcat populations in Wisconsin

JONATHAN GILBERT is Wildlife Section Leader with the Great Lakes Indian Fish and Wildlife Commission in Wisconsin. Jonathan received his B.A. from Washington and Jefferson College, his M.S. from Michigan State University, and his Ph.D. in Wildlife Ecology from the University of Wisconsin-Madison. He has been an active member of The Wildlife Society since 1977.

LLOYD B. KEITH is Professor Emeritus, Department of Wildlife Ecology, University of Wisconsin-Madison. Dr. Keith has had a long and distinguished career working primarily with snowshoe hares in boreal forest ecosystems. He and his students have published numerous articles detailing the population dynamics of cyclic hare populations and the predators that depend on them.

### Spatial resource overlap of bobcats and gray foxes in urban and rural zones of a national park

SETH RILEY grew up in Washington, D.C., and began working in wildlife biology there in 1987 at the National Park Service's Center for Urban Ecology. He received his B.A. in Human Biology with a concentration in Animal

Behavior and Ecology from Stanford University in 1988. He worked as a wildlife biologist at the Center for Urban Ecology from 1988–90, studying raccoon population and disease ecology, raccoon family relationships, and other urban wildlife issues including white-tailed deer impacts on vegetation. He attended graduate school at the University of California-Davis and received his Ph.D. in Ecology in 1999, conducting dissertation research on the ecology of bobcats and gray foxes in urban and rural zones of Golden Gate National Recreational Area. He then worked as a post-doctoral researcher in population genetics at University of California-Davis, studying hybridization between native and introduced tiger salamanders. He is currently with the National Park Service as the wildlife ecologist at Santa Monica Mountains National Recreational Area in southern California. He continues to be interested in urban wildlife ecology and the ecology and conservation of mammalian carnivores and reptiles and amphibians.

**Bobcat habitat use relative to human dwellings in southern Illinois**

See Nielsen and Woolf bios above...

**Spatio-temporal relationships among adult bobcats in central Mississippi**

MICHAEL J. CHAMBERLAIN is an Assistant Professor within the School of Forestry, Wildlife, and Fisheries at Louisiana State University. He received his Ph.D. in Forest Resources at Mississippi State University (MSU), an M.S. in Wildlife Ecology from MSU and a B.S. in Forestry and Wildlife Science from Virginia Tech. His research interests include upland avian ecology and management, influences of forest management on wildlife communities, predator-prey relationships, carnivore population ecology, and GIS applications to natural resource management. Mike currently serves as an Associate Editor for The Wildlife Society Bulletin and is faculty advisor for the Louisiana State University chapter of The Wildlife Society.

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**Multivariate habitat models for bobcats in southern forested lanscapes**

MIKE CONNER recieved his B.S. at the Univeristy of Tennessee-Martin and his M.S. and Ph.D. at Mississippi State University. Upon finishing his dissertation work, he became assistant professor at Arkansas Technical University. Mike is currently an assistant scientist at the Joseph W. Jones Ecological Research Center, where he studies predator ecology and forest-wildlife realtionships.

See Leopold and Chamberlain bios above...

**Utlity of bobcat observation reports for documenting presence of bobcats**

MARIE KAUTZ has worked over 20 years for the New York State Department of Environmental Conservation (NYSDEC), specializing in furbearer management for the last 7. She completed her B.S. in Wildlife Science at Cornell University and received an M.S. in Wildlife Biology from Colorado State University.

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BILL SHARICK graduated from Cornell University and has also been with the NYSDEC since 1972. He has spent most of his career working with waterfowl and furbearers. He is married with two children and his hobbies include trapping amd waterfowl and turkey hunting.

**Evolution of Wisconsin's bobcat harvest management program**

ROBERT E. ROLLEY is a wildlife population ecologist with the Wisconsin Department of Natural Resources. His responsibilities include research and consultation on the population ecology of Wisconsin wildlife, especially ungulates and furbearers, monitoring wildlife population trends, and modeling population response to management strategies. He previously (1983–92) worked as a wildlife biologist for the Indiana Division of Fish and Wildlife. He graduated in 1977 with a B.S. from the University of California at Davis and he received his M.S. from the University of Wisconsin-Madison (1979) and his Ph.D. from Oklahoma State University (1983).

BRUCE E. KOHN received his B.S. and M.S. degrees in Wildlife Management from the University of Minnesota. He has been employed as a research biologist for the Wisconsin Department of Natural Resources since 1970. Most of his research has involved developing and improving population monitoring and harvest programs for furbearers, bears, and wolves.

JOHN F. OLSON graduated from University of Wisconsin-Stevens Point with a B.S. in Wildlife Management in 1973. He worked with the Wisconsin Department of Natural Resources Forest Management and Wildlife Management programs in northern Wisconsin becoming the Forest Habitat Coordinator for northwestern Wisconsin in 1978. From 1979 to 1989, he was a field wildlife biologist for the WDNR located in northern Wisconsin with special emphasis on forest habitat and endangered species. From 1990 to 1993, he was an area wildlife supervisor in southwestern Wisconsin. In 1994, he became the Treaty Wildlife Biologist and in 1995 the statewide WDNR Furbearer Specialist.

**Perspectives on bobcat management in Illinois**

ROBERT D. BLUETT has worked for the Illinois Department of Natural Resources since 1989 and supervised its furbearer program since 1993. Program responsibilities include oversight of nuisance wildlife control activities, coordinating furbearer research and restoration, monitoring furbearer populations and harvest levels, and recom mending appropriate regulations for fur hunting and trapping. Bob received his B.A. in Biology from Ripon College and M.S. in Wildlife Management from the University of Wisconsin-Stevens Point. He is a certified Wildlife Biologist and served as president of the Illinois Chapter of The Wildlife Society from 1997 to 1998.

GEORGE F. HUBERT, JR. has been a wildlife biologist with the Illinois Department of Natural Resources' Fur bearer Program for 24 years and an affiliate research scientist in the Center for Wildlife Ecology, Illinois Natural History Survey, for 10 years. He has an M.S. in Wildlife Biology from Colorado State University and is a certified Wildlife Biologist. George's current professional interests include the ecology and management of furbearers, trap technology, and public outreach associated with fur hunting and trapping.

See Woolf bio above...

**Status and management of bobcats (*Lynx rufus*) in Pennsylvania.**

See Lovallo bio above...

## NOTES

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